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A Monograph of the Lichen Genus
Relicina (Parmeliaceae)

MASON E. HALE, JR.



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Mason E. Hale, Jr.

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ABSTRACT

Hale, Mason E., Jr. A Monograph of the Lichen Genus *Relicina* (Parmeliaceae). *Smithsonian Contributions to Botany*, number 26, 32 pages, 16 figures, 1975.—A revision on the world level is made for *Relicina*, a generic segregate of *Parmelia* characterized by having bulbate cilia on the lobe margins and by producing usnic acid in the cortex. Of the 24 species presently known, 19 occur in the Old World tropics, with the greatest concentration in the lowland dipterocarp forests, 3 are endemic to the New World tropics, and 2 occur in both the New and Old World outside of Africa. The most important taxonomic characters are type of rhizine (simple or branched), presence of coronate apothecia, isidia, and chemistry. The major chemical constituents are echinocarpic acid, fumarprotocetraric acid, and protocetraric acid. The genus is considered to be of fairly recent origin but rather conservative in terms of morphological and chemical evolution. Four new species, *R. amphithrix*, *R. incongrua*, *R. precircumnodata*, and *R. subconnivens*, are described and one new combination, *R. relicinula* (Müller Argau) Hale, is made.

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A Monograph of the Lichen Genus *Relicina* (Parmeliaceae)

Mason E. Hale, Jr.

Introduction

Relicina is a generic segregate of the collective genus *Parmelia*. It is characterized by marginal bulbate cilia and the constant occurrence of usnic acid, a yellow pigment, in the cortex. The genus includes 24 species, almost all of them occurring in tropical Southeast Asia. This paper is a monographic treatment of the genus based on herbarium and field studies.

The first species of *Relicina* was described by E. Fries as *Parmelia relicina* on the basis of a specimen from "Rawak" in 1825. Neither Linnaeus nor Acharius had seen any material belonging to this genus. Laurer described the second species, *P. limbata*, an Australian endemic, in 1827. This species is well known because it was issued in several widely distributed exsiccati.

In the remainder of the 19th century only five more taxa were discovered: *Parmelia abstrusa* Vainio, *P. circumnodata* Nylander, *P. relicinella* Nylander, *P. relicinula* Müller Argau, and *P. limbata* f. *isidiosa* Müller Argau (= *Relicina sydneyensis*). Between 1900 and 1964 an additional four taxa were described: *P. abstrusa* f. *laevigata* Lynge (= *Relicina subabstrusa*), *P. nigrociliata* Hillmann, *P. samoensis* Zahlbruckner, and *P. samoensis* var. *eximbricata* Gyelnik (= *Relicina eximbricata*). Hillmann (1940) recognized a natural relationship between six species described from the Old World and constructed a key to them.

In 1964 Hale and Kurokawa (1964) examined a

series of collections from the Bogor herbarium and described seven more species, mainly from Java and Borneo (Kalimantan and Sabah). Most of these, as with previous species, were known only from type collections. It became obvious during the course of their work, however, that these marginally bulbate species formed a natural group, quite distinct from section *Xanthoparmelia* where they had previously been classified. They recognized the 18 species then known as a series in subgenus *Parmelia* section *Imbricaria* subsection *Bicornutae*.

While this publication (Hale and Kurokawa, 1964) was actually in press, I had an opportunity to collect lichens in Malaysia, the Philippines, and Japan. What I discovered explained why this peculiar assemblage of species had been so poorly collected in the past and represented by so few herbarium specimens. *Relicina* inhabits canopy branches in the vast lowland dipterocarp forests from Burma to the Solomon Islands. I collected at logging heads where these giant trees, 60 m or more high, were being felled commercially. Most earlier collectors had obviously not been able to find (or did not try to find) felled trees. For example, many lichens were collected by botanists in the Philippines and studied by Vainio for his extensive Philippine lichen flora, yet he did not report a single species of *Relicina*, in reality the commonest foliose lichens in the Philippines! Another habitat where *Relicina* has proved abundant is the oak forests found at high elevation throughout southeastern Asia. These areas have not been visited by lichenologists either.

The most reassuring aspect of my field work was

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that all of the species described by Hale and Kurokawa were rediscovered, often in great abundance and comprising the major foliose element in lowland rain forest. As one might expect, more undescribed species were found. I described two species, *Parmelia fluorescens* and *P. malesiana* (Hale, 1965), and Kurokawa (1965) described other species from Japan (*P. echinocarpa* and *P. sub-turgida*). In the final revision of this monograph four more new species are being described to bring the total for the genus to 24 species.

ACKNOWLEDGMENTS.—I wish to thank the following curators of museums who kindly sent specimens on loan: Dr. S. Ahlner, Dr. T. Ahti, Dr. R. Alava, Dr. O. Almborn, Dr. C. E. Bonner, Mme. Jovet-Ast, Dr. R. A. Maas Geesteranus, Dr. H. Merxmüller, Dr. H. Riedl, and Dr. R. Santesson.

Dr. S. Kurokawa assisted with species descriptions, identification, and chemical studies both in 1960 in Washington and in 1964–1965 when I studied at the Tokyo National Science Museum. The field studies were supported by the National Science Foundation under the Japan-U.S. Cooperative Science Program and by the Smithsonian Research Foundation. In this connection I wish to express sincerest thanks to Dr. G. Velasquez and Dr. Flora Uyenco of the University of the Philippines, who arranged for trips to lumbering areas in the Philippines. I am also indebted to Mrs. Sheila Collonette for arranging a trip to Mt. Kinabalu, to Dr. W. Meijer for trips to eastern Sabah, and to Mr. J. Anderson for assistance in Sarawak. Dr. Manuel Lopez Figueiras kindly provided support and transportation in Venezuela. The project would never have been completed without the generous logistic support of lumber companies and forestry departments in the Philippines, Malaya, Sarawak, and Sabah.

The scanning-electron microphotographs were taken by Mr. Walter Brown of the Smithsonian Scanning-electron Microscope Laboratory. Herbarium specimens were photographed by the Smithsonian Photographic Services.

Morphological Characters

THALLUS ADNATION.—Most species are closely adnate and usually collected still attached to the bark. None have ascending lobes.

LOBE CONFIGURATION.—Species of *Relicina* are

extremely uniform in lobation. The lobes are generally narrow and sublinear, dichotomously branched, and contiguous. Small marginal lobules often develop.

VEGETATIVE PROPAGULES.—One of the most unusual features of *Relicina* is that no soredia are produced by any of the species. Soredia are usually the most common diaspore in the Parmeliaceae. Isidia, however, are produced by five species, *R. abstrusa*, *R. amphithrix* (Figure 1a), *R. circumnodata*, *R. planiuscula*, and *R. sydneyensis* (Figure 3i). The isidia are cylindrical and mostly unbranched but may become procumbent and lobulate in *R. amphithrix* and to a lesser extent in *R. planiuscula*. True lobules that do not originate from isidia are produced by *R. luteoviridis* (Figure 14e) and *R. schizospatha* (Figure 1b). Appressed palmately branched lobules (Figure 1c) are characteristic of some populations of *R. amphithrix*.

EPICORTEX AND CORTEX.—The internal structure of *Relicina* was studied by making longitudinal sections of the lobes and examining them under a scanning-electron microscope (SEM). All of the species are illustrated in Figures 1d–3i. I had previously determined with the SEM that *Relicina* has a pored epicortex and a basic palisade plectenchymatous upper cortex (Hale, 1972). More detailed investigations of internal structure for the purposes of this monograph have confirmed this structure. Most species have an irregularly arranged palisade layer 10–15 μm thick, rarely protruding downward to 20 μm (Figure 4c–h). The pored epicortex (Figure 4a,b) is about 0.6 μm thick as in other epicorticate genera (Hale, 1973). A particularly well-developed palisade structure, here called columnar, is characteristic of *R. fluorescens* and *R. planiuscula*, two related species with a coriaceous thallus. The upper cortex consists of packed columnar cells 20–25 μm high overlain by the epicortex (Figure 5a,c). A similarly well-developed columnar structure is known for *R. luteoviridis* (Figure 5b) and *R. subabstrusa* (Figure 5d), both smaller noncoriaceous species, where the cortex is about 20 μm thick.

ALGAL LAYER.—This layer is difficult to delimit in SEM photographs. It is often simply an area of loosely organized hyphae 10–20 μm thick, not sharply differentiated from the cortex above or the medulla below. Algae are scattered sparsely in this zone (Figure 1d,f).

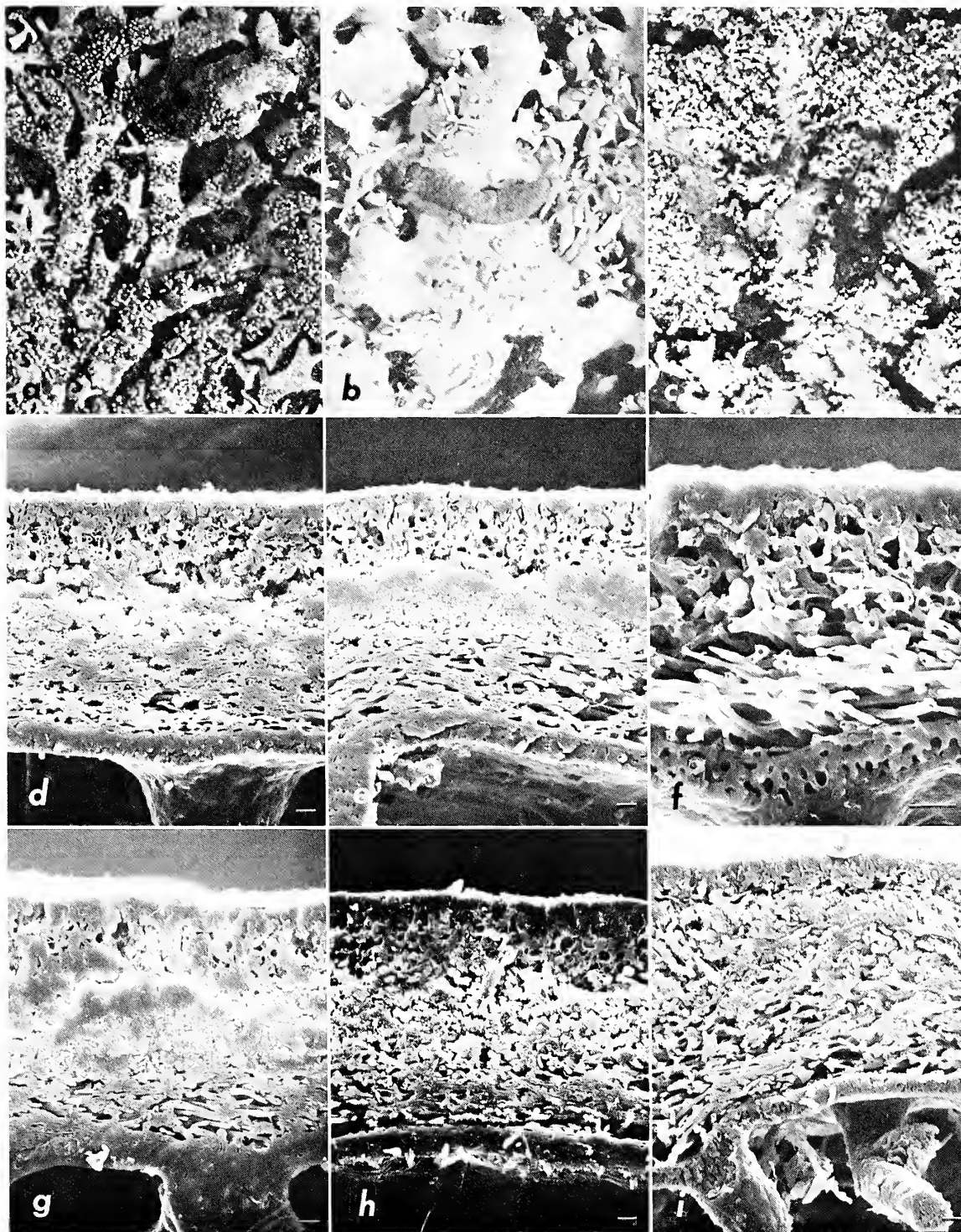


FIGURE 1.—Morphology of *Relicina*: a, isidia of *R. amphithrix* (Hale 30066) (about $\times 10$); b, lobules of *R. schizospatha* (Groenhart 2219) (about $\times 10$); c, lobules of *R. amphithrix* (Hale 30287) (about $\times 10$); d, *R. abstrusa* (Oberwinkler and Poelt); e, *R. acrobotrys* (Neervoort 60 pp.); f, *R. amphithrix* (Hale 30051); g, *R. circumnodata* (Hale 26580); h, *R. connivens* (Hoogland 4726); i, *R. echinocarpa* (Hale 29659). (Scale in lower right corner of d-i is 10 μm .)

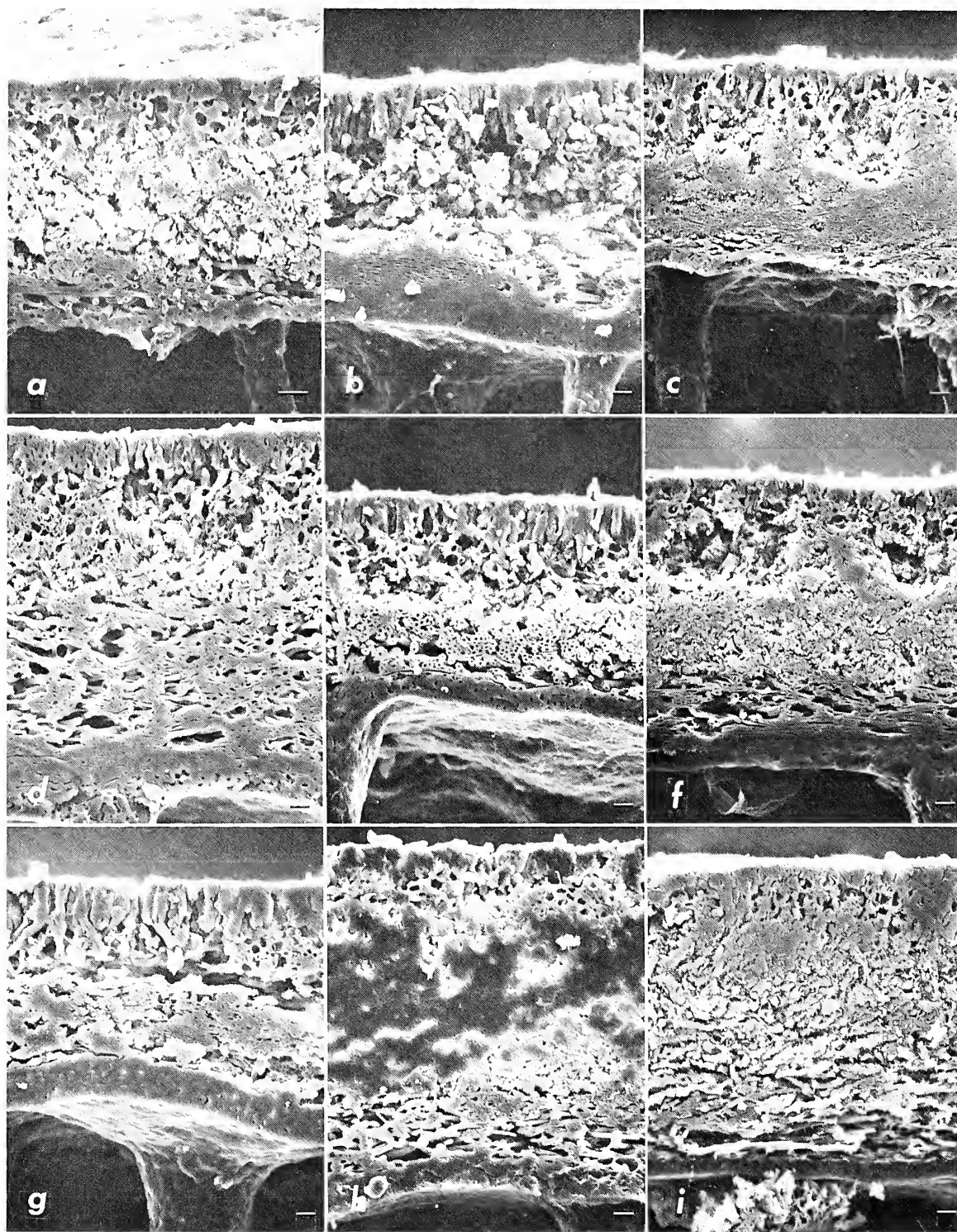


FIGURE 2.—Morphology of *Relicina*: a, *R. eximbricata* (Swanson C-745); b, *R. fluorescens* (Hale 29248); c, *R. incongrua* (Malme s.n.); d, *R. limbata* (Degelius A-368); e, *R. luteoviridis* (Meijer 13194d); f, *R. malesiana* (Hale 25370); g, *R. planiuscula* (Hale 26806); h, *R. precircumnodata* (Hale 25004a); i, *R. ramosissima* (Hale 30075). (Scale in lower right corner is 10 μ m.)

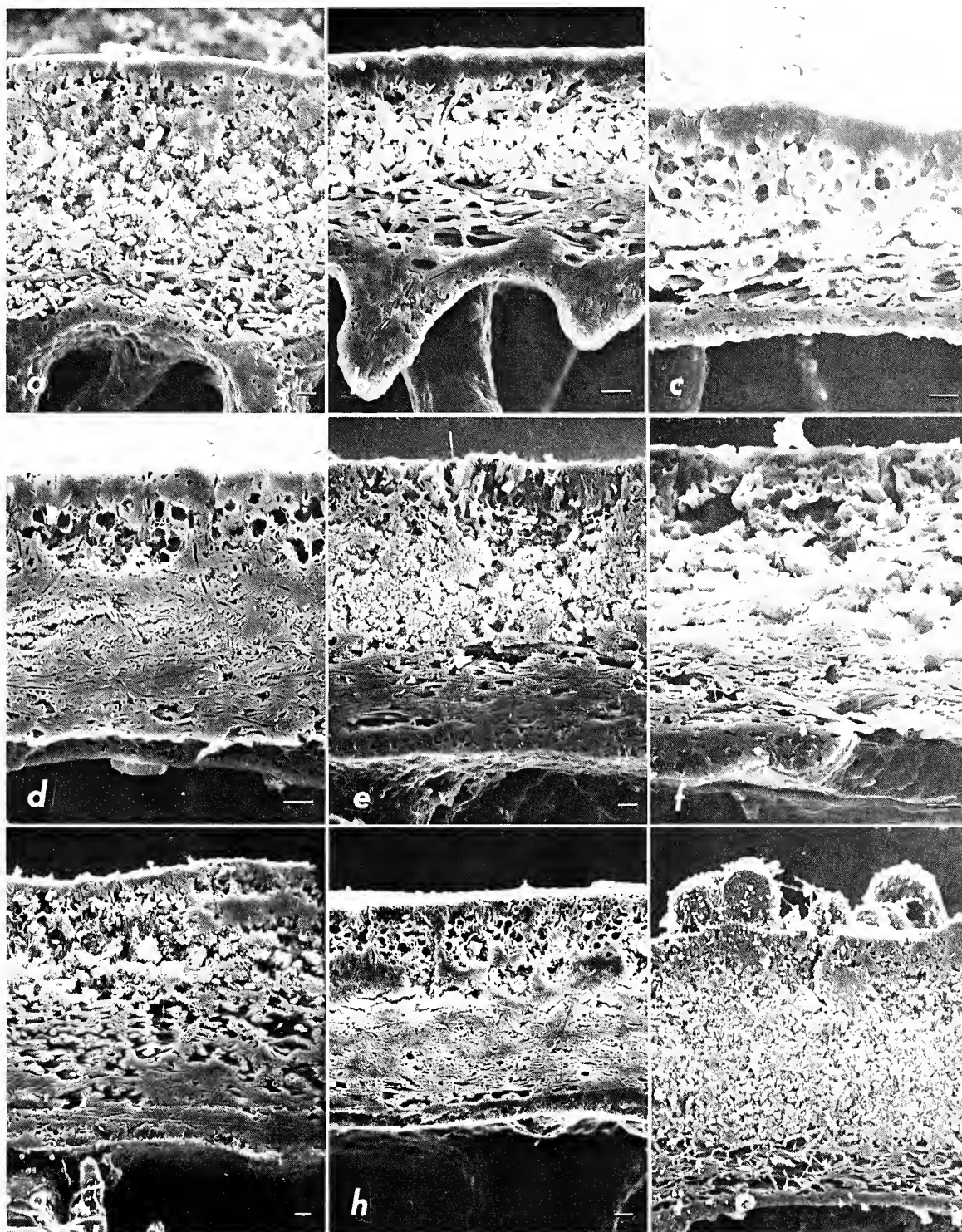


FIGURE 3.—Morphology of *Relicina*: a, *R. relicinella* (Nee and Mori 3766); b, *R. relicinula* (Hale 24402); c, *R. samoensis* (Hale 26955); d, *R. schizospatha* (Groenhart 2219); e, *R. subabstrusa* (Malme s.n.); f, *R. subconnivens* (Hale 30054); g, *R. sublanea* (Groenhart 8409); h, *R. sublimbata* (Kurokawa 1872); i, *R. sydneyensis* (Kurokawa 58622). (Scale in lower right corner is 10 μm .)

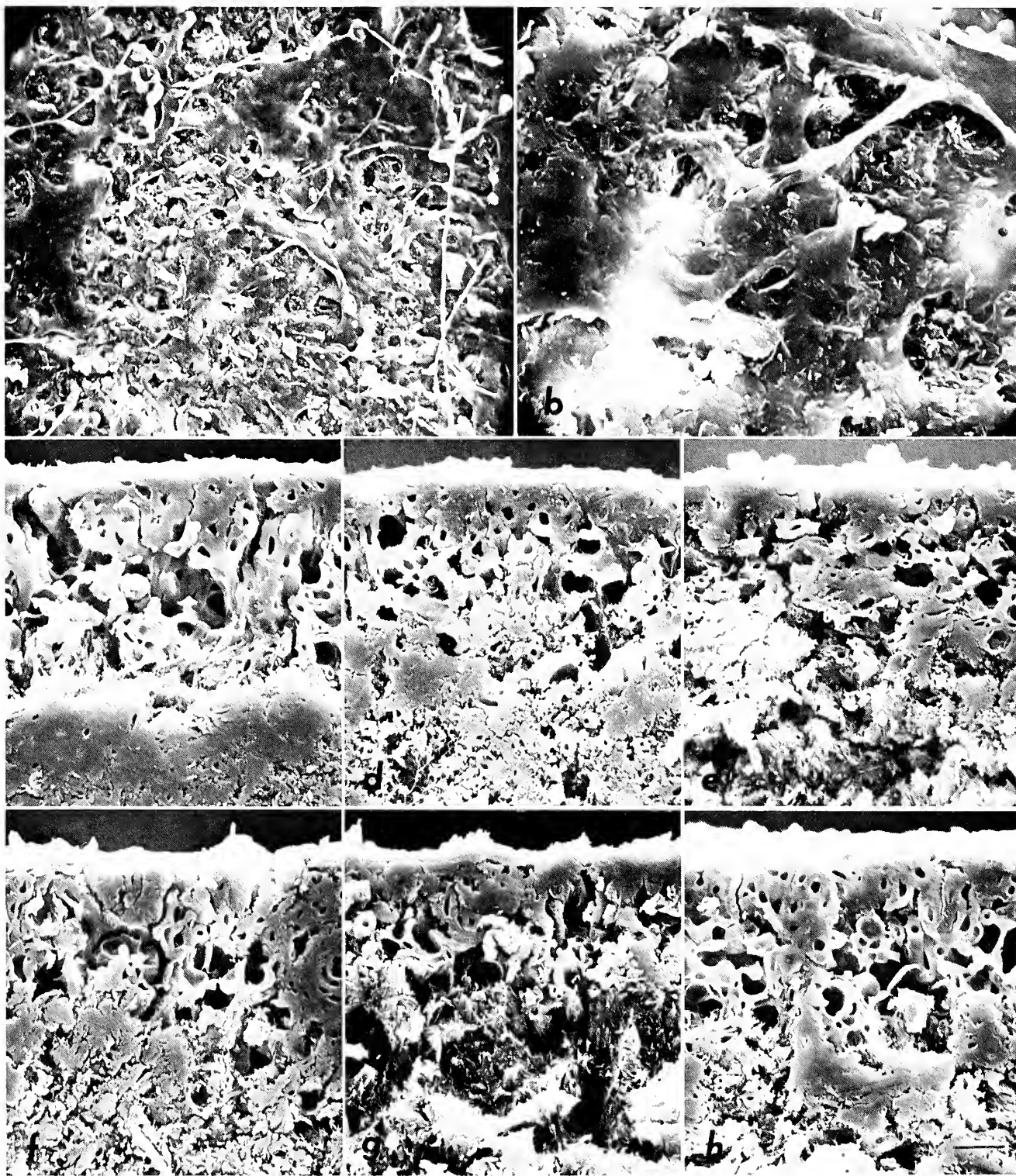


FIGURE 4.—Surface and upper palisade cortex structure in *Relicina*: a, b, surface of *R. incongrua* (Malme s.n.) $\times 500$ and $\times 2000$; c, *R. acrobotrys* (Neervoort 60 pp); d, *R. incongrua* (Malme s.n.); e, *R. malesiana* (Hale 25370); f, *R. ramosissima* (Hale 30075); g, *R. sublanca* (Groenhart 8409); h, *R. sublimbata* (Kurokawa 1872). (c–h all about $\times 1000$.)

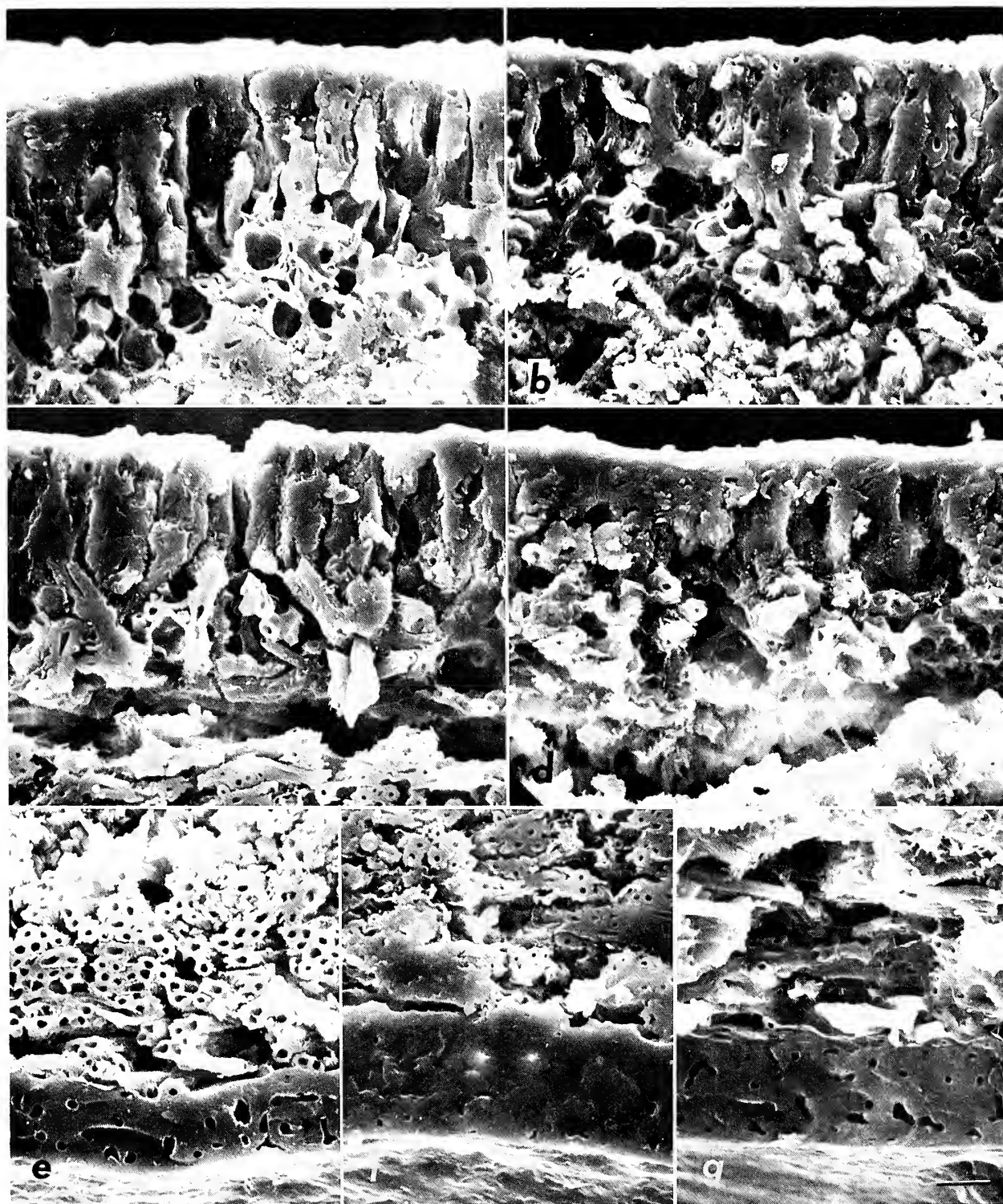


FIGURE 5.—Upper columnar cortex (a-d) and lower cortex (e-g) in *Relicina*: a, *R. fluorescens* (Hale 29248); b, *R. luteoviridis* (Meijer B 1946); c, *R. planiuscula* (Hale 26806); d, *R. subabstrusa* (Hale 26564); e, *R. luteoviridis* (Meijer B 1946); f, *R. planiuscula* (Hale 26806); g, *R. subabstrusa* (Hale 26564). (Scale of 10 μ m for all figures indicated in lower right corner of 5g).



FIGURE 6.—Bulbate cilia of *R. abstrusa* (about $\times 20$).

MEDULLA.—The medulla occupies about two-thirds of the thallus and varies considerably in density. In *R. amphithrix*, for example, a very small species, the hyphae are very loosely organized (Figure 1f). Most species, however, have a densely packed medulla (see in particular Figures 1g and 2h). Crystals of lichen substances encrust the hyphae, especially in the upper half of the medulla (Figure 3a,f).

LOWER CORTEX.—The lower cortex in all species consists of dense pachydermatous paraplectenchyma. It is up to 20 μm thick in larger coriaceous species, such as *R. planiuscula* (Figure 5f) but correspondingly thinner (10–16 μm) in less coriaceous species, such as *P. luteoviridis* (Figure 5e) or *R. subabstrusa* (Figure 5g).

BULBATE CILIA.—The marginal inflated bulbate cilia so characteristic of *Relicina* were probably first clearly recognized by Nylander when he described *Parmelia circumnodata* in 1883. These structures are produced along lobe margins with great regularity (Figure 6). They begin on new lobes as ordinary cilia but soon become basally inflated (Figure 7a). The ciliate tip may be lost or remain and even become densely branched. Mature globose bulbae are actually hollow (Figure 7b) and filled with a colorless fluid. The heavily carbonized walls are uniformly thickened and composed of densely conglutinated paraplectenchyma. A parallel-oriented prosoplectenchymatous structure, an orientation characteristic of cilia, can-

not be distinguished at the base but occurs farther along where the cilia were tapered. Inflated bulbae have undergone more differentiation than that involved simply in inflating the base of cilia. The function of marginal bulbate cilia is unknown. It is altogether possible, however, that they act as propagules. On rare occasions one can see lobules or even submacroscopic thalli that seem to have originated from detached bulbae. Since they do not contain algae, they would have to function as giant fungal diaspores and encounter suitable symbiotic algae before continuing growth.

LOWER SURFACE AND RHIZINES.—The lower surface is either black through carbonization or medium to very pale brown. The type of rhizine is broadly correlated with this color. Simple or sparsely branched rhizines often occur in species with a black lower surface, as in *R. abstrusa* (Figure 8a), *R. amphithrix*, *R. connivens*, *R. echinocarpa*, *R. eximbricata*, *R. fluorescens*, *R. incongrua*, *R. luteoviridis*, *R. planiuscula*, *R. relicinella*, *R. relicinula*, *R. samoensis*, *R. schizospatha*, *R. subabstrusa* (Figure 8c), and *R. subconnivens*. Two species with a brown lower surface also have simple rhizines: *R. limbata* (Figure 8b) and *R. sydneyensis*. Both *R. malesiana* and *R. sublimbata*, as well as some of the other lowland species, may have rather densely branched, almost squarrose rhizines, but these are always black and shiny without agglutination. Other species with a pale lower surface, including *R. acrobotrys* (Figure 8d), *R. circumnodata*, *R. precircumnodata* (Figure 8e), *R. ramosissima* (Figure 8f), and *R. sublanea* (Figure 8g), have densely branched, bushy, and in part agglutinated rhizines that form a woolly mat about 1 mm thick. The rhizines differ from squarrose types, such as one finds in *Parmelia sulcata* Taylor, in the pale color, the blunt rather than pointed tips, and the adherence of the various ramified parts. I have not seen this branching pattern outside of *Relicina*.

APOTHECIA.—Apothecia are very commonly produced in *Relicina*. Only two species, *R. luteoviridis* and *R. schizospatha*, lack them. Details on frequency are presented under the species descriptions. The discs are generally about 1–3 mm in diameter and imperforate (see, for example, Figures 13f, 14c, 15b, and 16b). The rim is smooth to crenate and either coronate, that is, provided with black bulbae (Figure 9) or ecoronate. While these

bulbae appear to be the same as bulbate cilia, they are in fact erect pycnidia (Figure 7*c,d*) with an apical pore, as most earlier workers seem to have concluded. The thallus also has the normal immersed pycnidia that one would expect to find in a parmelioid genus.

Bulbate cilia (retrorse rhizines) often develop around the base of both coronate and ecoronate

apothecia (Figure 9). These were first described by Laurer (1827) for *Relicina limbata*.

SPORES.—The asci contain the normal complement of eight spores as in other Parmeliaceae. *Relicina relicinella*, however, produces multispored asci with 16–32 spores. The spores are elliptical, ovoid, or nearly round, between 2–6 μm wide and 3–10 μm long. The one exception here is the un-

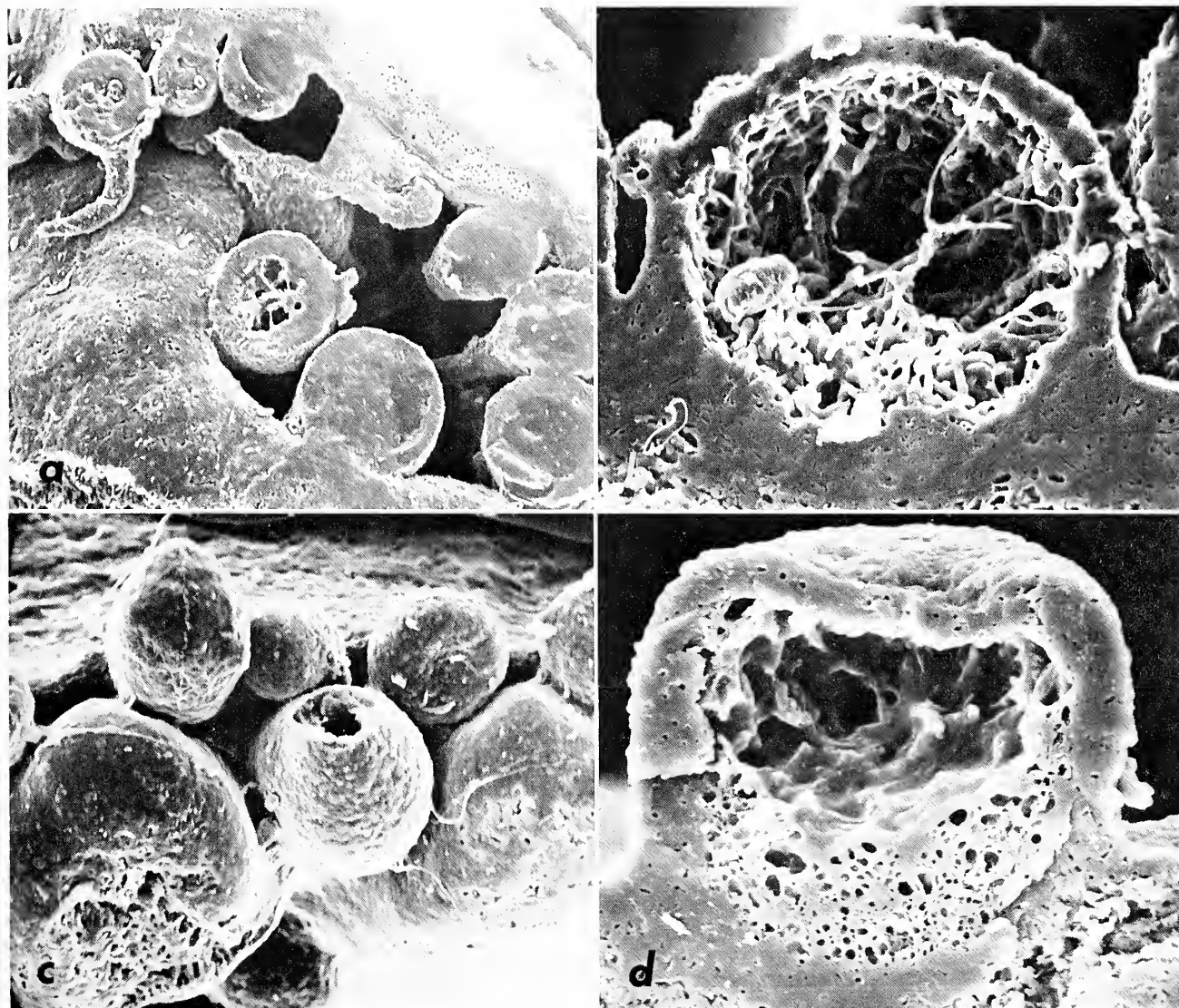


FIGURE 7.—Structure of bulbate cilia and amphithecial pycnidia: *a*, bulbate cilia on lobe margins of *R. sublanca* (Hale 30280) sectioned longitudinally ($\times 100$); *b*, longitudinal section of the base of a bulbate cilium of *R. precircumnodata* (Hale 25004a) ($\times 400$); *c*, amphithecial pycnidia of *R. circumnodata* (Hale 26433) ($\times 170$); *d*, vertical section of an amphithecial pycnidium of *R. circumnodata* (Hale 26433) ($\times 500$).

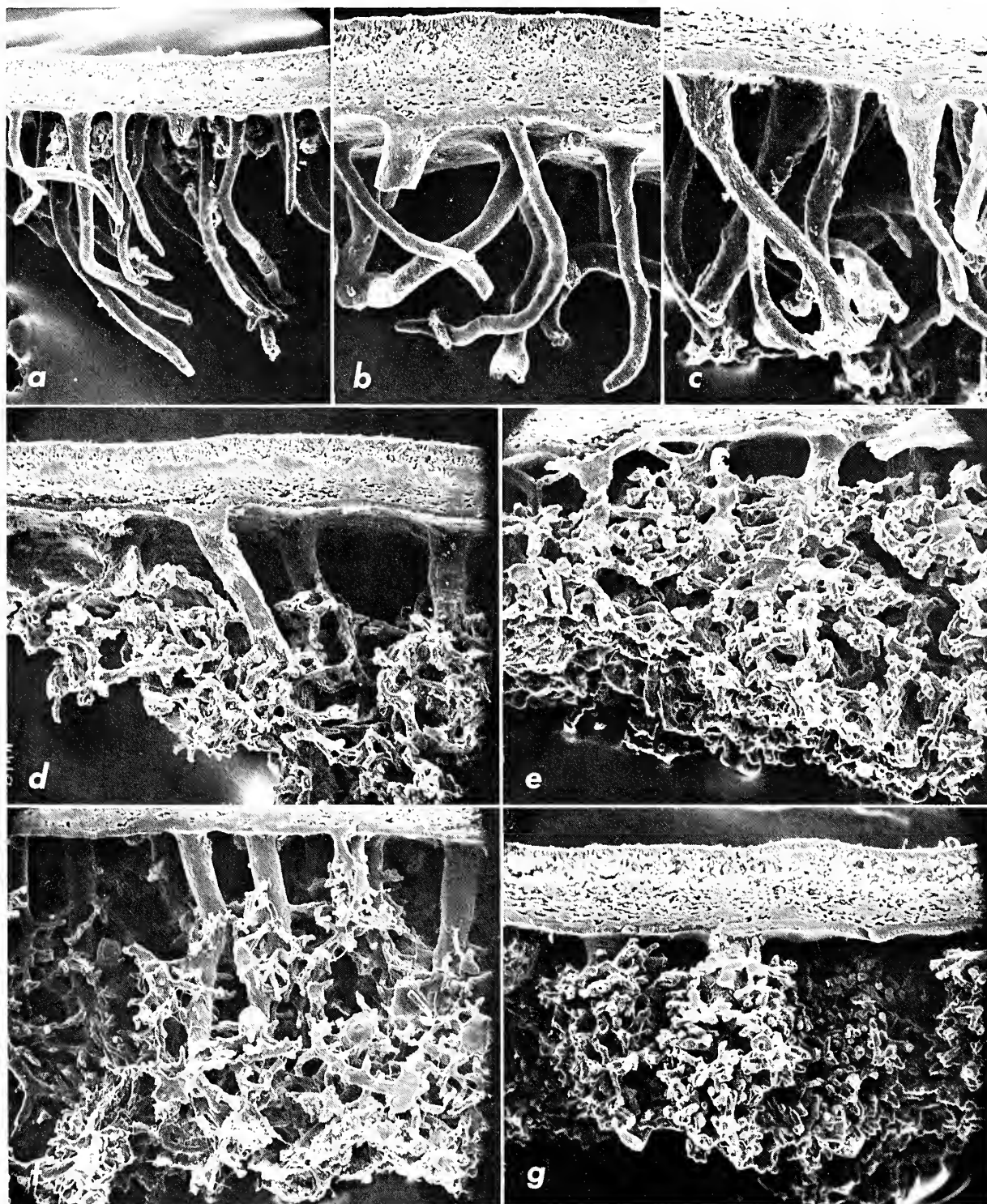


FIGURE 8.—Rhizine structure of *Relicina*: a, *R. abstrusa* (Oberwinkler and Poelt); b, *R. limbata* (Degelius A-368); c, *R. subabstrusa* (Malme s.n.); d, *R. acrobotrys* (Neervoort 60 pp.); e, *R. precircumnodata* (Hale 25004a); f, *R. ramosissima* (Hale 30075); g, *R. sublanea* (Groenhart 8409). (All about $\times 80$.)

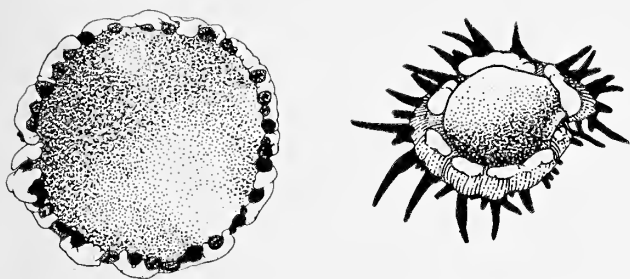


FIGURE 9.—Ornamentation of apothecia: coronate rim of *R. circumnodata* (left) and retrorse rhizines of *R. fluorescens* (both about $\times 15$). (Drawings by N. Halliday.)

usual bicornute spore of *R. precircumnodata* and its vegetative morph *R. circumnodata*. These are $2-3 \times 10-13 \mu\text{m}$ in size, similar to the spores of *Bulbothrix bicornuta* (Müller Argau) Hale.

Chemistry

The chemistry of *Relicina* was first summarized by Hale and Kurokawa (1964), who used microcrystal tests and later some thin-layer chromatography (TLC). All of the specimens have been reexamined, as far as possible, with TLC (Merck silica gel precoated plates) for this revision, using two solvent systems, hexane-ether-formic acid and benzene-dioxane-acetic acid. The substances identified in *Relicina* are listed below. Species with chemical strains are listed two or more times.

Alectoronic acid: *R. fluorescens*.

Atranorin: Sporadically produced in *R. acrobotrys*, *R. limbata*, *R. planiuscula*, and *R. sydneyensis*.

Barbatic acid: *R. abstrusa*, *R. acrobotrys*, *R. incongrua*.

Caperatic acid: *R. subconnivens*.

Consalazinic acid: *R. acrobotrys*.

Diffractaic acid: *R. abstrusa*, *R. incongrua*.

Echinocarpic acid: *R. amphithrix*, *R. echinocarpa*, *R. fluorescens*, *R. planiuscula*, *R. samoensis*, *R. schizospatha*.

4-O-Demethylbarbatic acid: *R. abstrusa*, *R. acrobotrys*, *R. incongrua*.

Fumarprotocetraric acid: *R. eximbricata*, *R. malesiana*, *R. ramosissima*, *R. relicinella*, *R. sublimbata*.

Gyrophoric acid: *R. luteoviridis*.

Norstictic acid: *R. abstrusa*, *R. limbata*, *R. subabstrusa*, *R. sydneyensis*.

Protocetraric acid: *R. circumnodata*, *R. precircumnodata*, *R. sublanea*.

"Quintaria" unknown: *R. abstrusa*.

Protolichesterinic acid: *R. connivens*.

Salazinic acid: *R. abstrusa*, *R. acrobotrys*, *R. echinocarpa*, *R. subabstrusa*.

Stictic acid: *R. limbata*, *R. sydneyensis*.

Succinprotocetraric acid: *R. eximbricata*, *R. ramosissima*, *R. sublimbata*.

Usnic acid: All species of *Relicina*.

P+ unknown: *R. relicinella*.

C+ unknown: All species containing echinocarpic acid.

Other unknowns: *R. fluorescens* (with alectoronic acid).

No medullary substances: *R. amphithrix*, *R. relicinula*.

The identification of these acids with TLC presents no special problems. The protocetraric acid and related acids are separated most effectively in hexane, where fumarprotocetraric acid is highest, and succinprotocetraric acid lowest with protocetraric acid falling between them. Separation improves with an extra 10–20 ml of ether added to the solvent. Both barbatic and 4-O-demethylbarbatic acids occur in trace amounts; diffractaic acid occurs in high concentration. Species containing echinocarpic acid produce several additional spots, none of which have been identified.

An unusual feature of *Relicina* is the predominance of P+ depsidones and the unidentified echinocarpic acid, which appears to be P+ depside. Echinocarpic acid seems to be especially characteristic of *Relicina*, although it occurs rarely in *Hypotrachyna*, usually in conjunction with barbatic acid (Culberson and Hale, 1973), and in *Parmotrema* along with protocetraric acid (Hale, 1971).

The substances occur in several patterns. A common one is acid A or acid A + B, as in *R. acrobotrys* (salazinic acid or salazinic acid with barbatic acid). An acid-deficient pattern (acid A or no acid) is evident in *R. amphithrix* (no medullary substance or echinocarpic acid present). Both *R. echinocarpa* and *R. fluorescens* show the pattern acid A, acid A + B, and acid B. With *R. echinocarpa* this involves salazinic and echinocarpic acids and with *R. fluorescens* alectoronic and echinocarpic acids. Other examples of variation are discussed under the various species. I prefer not to treat these chemical populations as species because of the absence of any strong correlating morphological or geographical characters.

Ecology and Habitats

Relicina occupies two main habitats, the canopy branches of dipterocarps and other trees in the lowland rain forest and the trunk and branches of

Quercus at high elevations. A few species grow in secondary forests on trees such as coconut or even on rocks.

The typical lowland dipterocarp forests occur in dense stands from sea level to less than 1000 m elevation. The highest locality at which I collected on dipterocarp was 850 m in Negros Occidental, Philippines. Those species which occur in this elevational range (and often only up to 400 m) include *R. circumnodata*, *R. connivens*, *R. malesiana*, *R. precircumnodata*, *R. ramosissima*, *R. relacinula*, *R. subabstrusa*, *R. subconnivens*, and *R. sublanea*. In the New World one finds *R. incongrua* in a similar range of elevation. In almost all cases I collected these species in areas where trees were being felled commercially, and since the dipterocarp forests do not usually regenerate, *Relicina* could become extinct as the forests are timbered throughout southeast Asia.

Oak and, on Luzon, Philippines, *Pinus* make up the typical vegetation above about 1400 m elevation on mountains in Southeast Asia. The characteristic species here are *R. acrobotrys*, *R. fluorescens*, *R. luteoviridis*, *R. planiuscula*, and *R. schizospatha*. These oak forests are being cut over for vegetable farms and as with the dipterocarp forests many of the *Relicina* species will eventually become extinct.

Several temperate species occur on trees and rocks at relatively low elevation. These include *R. echinocarpa*, *R. limbata*, and *R. sydneyensis*. Also occurring at low elevation but in disturbed forests in tropical regions are *R. samoensis* and *R. eximbricata*. *Relicina sublimbata* seems to occur in drier subtropical areas of Burma and Thailand at mid elevations.

Two species, one restricted to Asia (*R. amphithrix*) and the other pantropical outside of Africa (*R. abstrusa*), have very great elevational ranges, from 150 m to over 1600 m.

Phytogeography

The most distinctive feature of *Relicina* is the high degree of endemism in Southeast Asia. Outside of *R. abstrusa* and *R. subabstrusa*, which occur in the Neotropics as well as in Asia, and three neotropical endemics (*R. eximbricata*, *R. incongrua*, *R. relicinella*), all remaining 19 species occur only in the Old World. At the same time the genus is

as yet unknown in Europe, India and central Asia, and Africa, except for a single isolated collection of *R. subabstrusa* on the Comoro Islands near Madagascar.

The genus obviously evolved in the ancient dipterocarp forests of Southeast Asia. The endemic neotropical species may be remnants of older more widespread species, although they are unrelated to any species now found in the Old World. Alternatively they may have evolved separately in the New World where conditions have obviously not been favorable for rapid evolution and expansion of the genus.

The number of species known in various geographic areas is summarized in Figure 10. The actual species by region are tabulated as follows:

- Japan: *R. abstrusa*, *R. echinocarpa*, *R. planiuscula*, and *R. sydneyensis*.
 Taiwan: *R. abstrusa*, *R. malesiana*, *R. planiuscula*, *R. subabstrusa*, and *R. sydneyensis*.
 Philippines: *R. abstrusa*, *R. amphithrix*, *R. circumnodata*, *R. connivens*, *R. malesiana*, *R. planiuscula*, *R. precircumnodata*, *R. ramosissima*, *R. relacinula*, *R. samoensis*, *R. schizospatha*, *R. subabstrusa*, and *R. sublanea*.
 Malaya: *R. abstrusa*, *R. amphithrix*, *R. circumnodata*, *R. planiuscula*, *R. ramosissima*, *R. relacinula*, *R. schizospatha*, *R. subconnivens*, and *R. sublanea*.
 Indonesia: *R. abstrusa*, *R. acrobotrys*, *R. connivens*, *R. planiuscula*, *R. ramosissima*, *R. relacinula*, *R. samoensis*, *R. schizospatha*, *R. sublanea*, and *R. sydneyensis*.
 Sarawak: *R. abstrusa*, *R. circumnodata*, and *R. subabstrusa*.
 Sabah: *R. acrobotrys*, *R. amphithrix*, *R. fluorescens*, *R. luteoviridis*, *R. malesiana*, *R. planiuscula*, *R. ramosissima*, and *R. schizospatha*.
 New Guinea: *R. connivens*, *R. fluorescens*, and *R. malesiana*.
 Australia: *R. limbata*, *R. subabstrusa*, and *R. sydneyensis*.
 Pacific Islands: *R. connivens* and *R. samoensis*.
 Thailand-Burma: *R. sublimbata*.
 Comoro Islands: *R. subabstrusa*.
 U.S.A.: *R. abstrusa* and *R. eximbricata*.
 Mexico: *R. abstrusa*.
 West Indies: *R. abstrusa* and *R. eximbricata*.
 Panama: *R. abstrusa* and *R. incongrua*.
 Colombia: *R. abstrusa*, *R. relicinella*.
 Venezuela: *R. abstrusa*.
 Brazil: *R. abstrusa*, *R. incongrua*, *R. relicinella*, and *R. subabstrusa*.
 Paraguay: *R. abstrusa* and *R. subabstrusa*.
 Argentina: *R. abstrusa*.

The commonest species of *Relicina* are as follows with number of collections examined: *R. subabstrusa* (52), *R. amphithrix* (43), *R. circumnodata* (40), *R. planiuscula* (37), *R. relacinula* (31), *R. abstrusa* (26), and *R. schizospatha* (20). Rarities

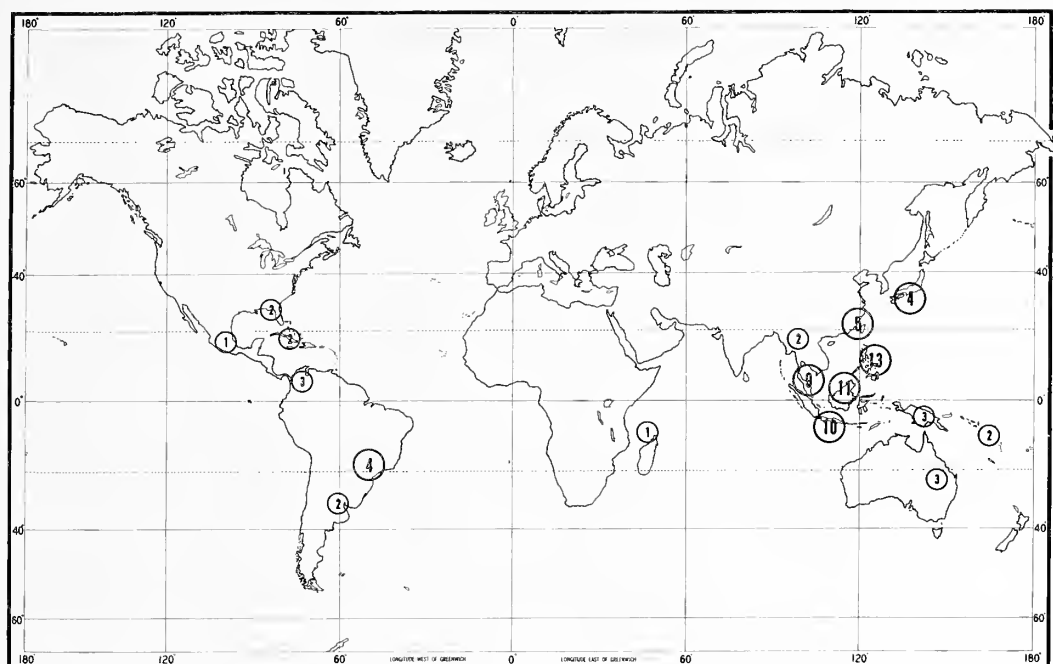


FIGURE 10.—Number of *Relicina* species recorded in various major geographical areas.

include *R. luteoviridis* (3), *R. precircumnodata* (3), and *R. subconnivens* (1).

The localities where especially large numbers of specimens were collected include logging areas in Negros Occidental, Philippines (44 collections), Selangor, Malaya (40), and Mountain Province, Philippines (36). The richest localities had six or seven species each with considerable differences in species composition.

Evolution and Speciation

Very little is known or even hypothesized about evolution and speciation in lichens. Lacking any fossil record, lichenologists are left with few clues that can be used to trace evolution of species and genera. Chemistry has proven to be a valuable independent check in some groups, especially the Parmeliaceae. I have already discussed in some detail the evolution of species in *Hypotrachyna* (Hale, 1975), where hybrid chemistries and rich development of vegetative morphs permit one to draw a fairly complete picture of speciation. By comparison, *Relicina* has fewer vegetative morphs and the chemistry is less varied. The structure of

the most characteristic acid, echinocarpic acid, is as yet unknown. The following discussions, therefore, will cover only the more obvious lines of evolution.

MORPHOLOGICAL EVOLUTION

FORMATION OF MORPHS.—A vegetative morph is defined as an isidiate or sorediate population which is absolutely identical in chemistry and morphology (excepting the diaspores) to a fertile, nonisidiate or nonsorediate parent population. A discussion of the development of the theory of morphs in lichens is presented by Hale (1975). In *Hypotrachyna*, for example, more than half of the speciation can be attributed to the formation of morphs. A similar situation is known in *Parmotrema* (Hale, 1965a; Culberson, 1973).

Relicina is exceptional in that soredia are not formed by any of the species. Isidia do occur, however, in five species, and four of these can be paired with nonisidiate sexual morphs:

- R. abstrusa*—*R. subabstrusa*
- R. circumnodata*—*R. precircumnodata*
- R. planiuscula*—*R. fluorescens* (echinocarpic acid population)
- R. sydneyensis*—*R. limbata*

The acid deficient population of *R. amphithrix* is closely related to nonisidiate *R. relacinula* and may represent a vegetative morph, but variation in isidia and lobule development is so great that the evidence for a direct derivation is poor.

RHIZINES.—The type of rhizine, simple or branched, appears to be an important character. The five species with branched agglutinated, pale rhizines seem to form a close group that originated in and has not migrated out of the dipterocarp forests. One, *R. acrobotrys*, occurs only in high elevation forests and, perhaps significantly, is chemically completely distinct from the other four species in containing salazinic and barbatic acids. The other species contain protocetraric acid or fumarprotocetraric acid and occur only at low elevations. One series, including *R. ramosissima* and *R. sublanea*, is ecoronate and has small ovoid spores; the other series, including *R. precircumnodata* and its isidiate morph *R. circumnodata*, is coronate and has cornute spores. The main lines of evolution here seem to be ecological isolation and differentiation in apothecial and spore characters (Figure 11).

CORONATE APOTHECIA.—I am assuming that ecoronate species are more primitive than coronate species and gave rise by mutation to coronate species. This seems fairly evident in the *R. sublanea*—*R. circumnodata* group discussed above where the coronate condition is paralleled by spore evolution and where chemistry is not significantly changed. A somewhat different pattern can be

seen in *R. connivens* (ecoronate) and *R. subconnivens* (coronate) where the spores have not changed but the chemistry is altered (protolichesternic acid versus caperatic acid). In most other species of *Relicina*, however, parallel ecoronate–coronate populations are not closely matched, or as in the *R. eximbricata* group in the New World no ecoronate parent populations are extant. Conversely no coronate species have evolved from the *R. limbata* group.

CHEMICAL EVOLUTION

Chemical evolution is presumed to involve genetic processes that lead to differentiation of a parent species into two or more chemical populations. The patterns may be extremely clear-cut and easy to follow, as in *Hypotrachyna* (Hale, 1975), or too complex to interpret. *Relicina* has a less varied chemistry but several examples can be given. One is the difference between the two main populations of *R. abstrusa* and *R. subabstrusa*. All specimens of these two related species contain approximately equal amounts of norstictic acid and salazinic acid in the New World. Most specimens in the Old World, however, even though externally indistinguishable from those in the New World, usually lack salazinic acid or have at most trace amounts. The constancy of the difference suggests that the two major populations have been isolated for a long period and that no genetic interchange has occurred during this period of isolation. The New World populations have in fact begun to evolve in another direction, if we correctly interpret the evidence from a single Brazilian collection, which contains diffractaic and barbatic acids, indicating a backcross with a parent morph containing diffractaic acid, similar for example to *R. incongrua*. If true, we can expect other chemical evolution in the New World, especially since apothecia are common in both the isidiate and nonisidiate populations, whereas the more conservative Old World isidiate population usually lacks apothecia and gives no evidence of continuing chemical evolution.

Another example of possible backcrossing can be cited for the *R. fluorescens* group. The two species here, *R. fluorescens* and *R. planiuscula*, are morphologically very close because of the strongly developed columnar cortex and similar habitats at

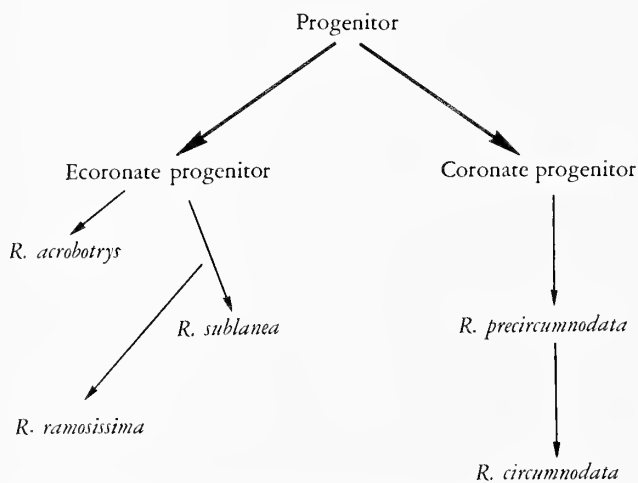


FIGURE 11.—Hypothetical evolution of species with branched, pale rhizines.

higher elevations. The presumptive parent, *R. fluorescens*, has a complex chemical population structure, aleotoronic acid alone, echinocarpic acid alone, and the two acids occurring jointly (Figure 12). The three populations occur together in significant numbers in Sabah. The vegetative morph, *R. planiuscula*, contains only echinocarpic acid. If we are correct in assuming that *R. planiuscula* evolved from *R. fluorescens* or a sexual morph similar to it, as shown in Figure 12, then the morph must have developed before *R. fluorescens* underwent chemical evolution. A corollary of this assumption is that the progenitor population contained echinocarpic acid. Perhaps the aleotoronic acid-containing populations of *R. fluorescens* have not had time to develop isidiate morphs, or if they have evolved they cannot, for reasons we cannot even guess at this time, compete with the now widespread echinocarpic acid-containing morph *R. planiuscula*.

Another example of how species have diverged slightly in chemistry and apparently become reproductively isolated is *R. eximbricata* and *R. relicinella* in the New World. While these externally similar species share the production of fumarprotocetraric acid, *R. eximbricata* also produces succinprotocetraric acid, while *R. relicinella* contains an unidentified P+ compound, also apparently related to protocetraric acid. More significantly, *R. relicinella* has multispored asci.

The species containing echinocarpic acid form the nucleus of the genus in Southeast Asia. We cannot speculate on the chemical evolution of this group until the molecular structure of echinocarpic acid is determined.

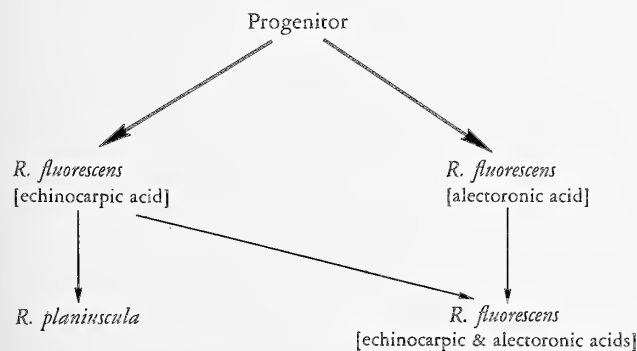


FIGURE 12.—Hypothetical evolution of chemical populations in *R. fluorescens* and *R. planiuscula*.

A common situation in *Relicina* is the differentiation of species into parallel chemical groups with various combinations of fumarprotocetraric acid and other substances. For example *R. sublimbata* and *R. malesiana* are essentially identical but *R. sublimbata* produces succinprotocetraric acid along with fumarprotocetraric acid, while *R. malesiana* produces only fumarprotocetraric acid. In this instance the species have a different geographic range, *R. sublimbata* occurring in Burma and Thailand, *R. malesiana* from Taiwan south to New Guinea apart from the Asian mainland.

Position of *Relicina* in the Parmeliaceae

Relicina has an isolated position in the Parmeliaceae because of its morphology and phytogeography. First, it has nothing to do with *Xanthoparmelia*, with which it shares only the yellow cortical pigment usnic acid. The only closely related genus is *Bulbothrix* (Hale, 1974), which also has marginal bulbate cilia and coronate apothecia but which produces only atranorin in the cortex. *Bulbothrix*, however, is rare in the range of *Relicina*. Only *B. subdissecta* (Nylander) Hale and *B. pigmentacea* (Hale) Hale occur in the lowland rain forests of Southeast Asia and *B. subinflata* (Hale) Hale in oak forests where one finds *Relicina*. *Bulbothrix* is largely a genus of the drier subtropical zones, being especially common in southeastern United States and Africa. It generally has larger spores, 12–19 μm long, twice the average size of those in *Relicina*, although a few species do have spores only 2–4 μm long. The chemistry of *Bulbothrix* is different in many respects and there is little evidence of any significant chromosomal exchange with *Relicina* that might appear in the chemistry. Many species of *Bulbothrix*, for example, have gyrophoric or salazinic acid, both of these very rare in *Relicina*. No barbatic, diffractaic, echinocarpic, fumarprotocetraric, or stictic acids are produced. On the other hand, *Bulbothrix* produces lecanoric, lobaric, and colensoic acids, all unknown in *Relicina*. I would argue then that *Bulbothrix* and *Relicina* as they presently stand are not closely related biologically. This does not rule out the possibility that they have a distant common origin which may have centered on the usnic acid-atranorin split.

Key to Species of *Relicina*

1. Thallus isidiate, isidiate-lobulate, or lobulate.
 2. Isidia distinct, cylindrical.
 3. Lower surface pale brown.
 4. Rhizines densely branched. 4. *R. circumnodata*
 4. Rhizines simple. 24. *R. sydneyensis*
 3. Lower surface black.
 5. Lobes very narrow and appressed, 0.5–1.0 mm wide 3. *R. amphithrix*
 5. Lobes broader, adnate, 1–3 mm wide.
 6. Medulla K+ red. 1. *R. abstrusa*
 6. Medulla K–. 13. *R. planiuscula*
 2. Isidia becoming dorsiventral and lobulate or only lobules present.
 7. Lobes narrow and appressed, 0.5–1.0 mm wide. 3. *R. amphithrix*
 7. Lobes broader and adnate, 1–3 mm wide.
 8. Medulla C+ red; lobules densely developed. 11. *R. luteoviridis*
 8. Medulla C– or dull yellowish red (and P+ red); lobules not dense.
 9. Thallus coriaceous; upper cortex columnar. 13. *R. planiuscula*
 9. Thallus thinner; upper cortex not columnar. 19. *R. schizospatha*
1. Thallus lacking isidia and lobules (some adventitious marginal lobules may be present).
 10. Lower surface tan to pale brown.
 11. Rhizines simple. 10. *R. limbata*
 11. Rhizines densely branched.
 12. Medulla K+ red. 2. *R. acrobotrys*
 12. Medulla K–.
 13. Apothecia present, coronate. 14. *R. precircumnodata*
 13. Apothecia ecoronate or lacking.
 14. Protocetraric acid present. 22. *R. sublanea*
 14. Fumarprotocetraric acid present. 15. *R. ramosissima*
 10. Lower surface black.
 15. Apothecia present, coronate.
 16. Medulla K+ red. 20. *R. subabstrusa*
 16. Medulla K–.
 17. Medulla P–.
 18. Diffractaic acid present; New World species. 9. *R. incongrua*
 18. Diffractaic acid absent; Old World species.
 19. Lobes narrow and appressed, 0.5–1.0 mm wide. 17. *R. relacinula*
 19. Lobes broader and adnate, 1–3 mm wide. 21. *R. subconnivens*
 17. Medulla P+ orange red.
 20. Echinocarpic acid present; Old World species. 18. *R. samoensis*
 20. Fumarprotocetraric acid present; New World species.
 21. Spores 8/ascus. 7. *R. exinbricata*
 21. Spores 16–32/ascus. 16. *R. relacinella*
 15. Apothecia ecoronate or lacking.
 22. Medulla K+ red.
 23. Salazinic acid only present. 6. *R. echinocarpa*
 23. Norstictic and salazinic acids present. 20. *R. subabstrusa*
 22. Medulla K–.
 24. Medulla P–.
 25. Lobes narrow and appressed, 0.5–1 mm wide. 17. *R. relacinula*
 25. Lobes broader and adnate, 1–3 mm wide.
 26. Upper cortex columnar; alectoronic acid present. 8. *R. fluorescens*
 26. Upper cortex not columnar; protolichesterinic acid present. 5. *R. connivens*
 24. Medulla P+ orange red.
 27. Echinocarpic acid present.
 28. Upper cortex columnar. 8. *R. fluorescens*
 28. Upper cortex not columnar. 6. *R. echinocarpa*

27. Fumarprotocetraric acid present.
 29. Succinprotocetraric acid present. 23. *R. sublimbata*
 29. Succinprotocetraric acid lacking. 12. *R. malesiana*

Species Treatment

Relicina

Relicina (Hale and Kurokawa) Hale, 1974:484.

Parmelia subgenus *Parmelia* section *Imbricaria* subsection
Bicornutae series *Relicinae* Hale and Kurokawa, 1964:135.

Type-species: *Parmelia relicina* Fries, 1825:283.

My typification of the genus (Hale, 1974) was not completely accurate since *Parmelia relicina* must be designated as the type-species even though it becomes a tautonym when transferred to *Relicina*. Furthermore, my typification of *Parmelia eumorpha* Hepp, based on an incorrectly determined specimen in the Rijksherbarium (L), which I considered to be a valid type, is in error. As Müller Argau (1882) had pointed out, Hepp's species is a *Coccocarpia* and the specimen which Müller Argau examined (in G) is indeed a *Coccocarpia*, although the same number in L is a *Relicina* species. Finally, Hepp's protologue obviously refers to a nonparmelioid genus.

The species are listed alphabetically in the listing below. All collections by Hale are deposited in the National Museum of Natural History, Smithsonian Institution, and the herbarium acronym (US) is not given.

1. *Relicina abstrusa*

FIGURE 13a

Relicina abstrusa (Vainio) Hale, 1974:484.

Parmelia abstrusa Vainio, 1890:64 [type-collection: Caraça, Minas Gerais, Brazil, Vainio 1347 (not 1346) (TUR, lectotype; UPS, isoelectotype)].

Thallus closely adnate on bark or rocks, 6–10 cm in diameter, pale chartreuse yellow; lobes sublinear, 1–2 mm wide; upper surface plane to convex, continuous or faintly maculate, moderately isidiate, isidia short, mostly simple; bulbate cilia moderately inflated; lower surface black and rhizinate, the rhizines simple, shiny (Figure 8a). Apothecia adnate, 1–4 mm in diameter, coronate, basally retrorsely rhizinate, the amphithecium

isidiate, the disc carob brown; spores 8, 4–5 × 5–6 µm.

CHEMISTRY.—Medulla K+ yellow turning red, C–, KC–, P+ orange, norstictic and usnic acids with or without salazinic acid and very rarely with diffractaic acid and a trace of barbatic acid and 4-0-demethylbarbatic acid. A “quintaria” unknown, the reddish pink spot just below norstictic acid in both solvent systems, occurs in about one-quarter of the specimens.

REMARKS.—This is a very common species in both the New World and the Old World. As with *R. subabstrusa*, the presumptive nonisidiate parent, the New World specimens produce norstictic and salazinic acids in nearly equal concentration, but salazinic acid is either absent or present in trace amounts in Old World specimens. The two populations also differ in elevational range. In Southeast Asia *R. abstrusa* occurs commonly from 100 m to 1400 m elevation. The same species in South America ranges from 700–2450 m. Apothecia are much more common in the New World populations (53% frequency) than in the Old World (7% frequency).

One specimen from Brazil (*Lichenes austro-americi* 95) contained diffractaic acid and a trace of barbatic acid in addition to the main components listed above. This unusual combination of acids could have originated as a backcross with a species such as *R. incongrua*, which contains only diffractaic and barbatic acids.

Vainio (1890) considered *Parmelia limbata* f. *isidiosa* Müller Argau to be a synonym of *P. abstrusa*, but Müller's taxon is now recognized as *Relicina sydneyensis*. Asahina (1951) identified norstictic and stictic acids in Japanese specimens, which he identified as *P. abstrusa* and these too represent *Relicina sydneyensis*.

SPECIMENS EXAMINED.—Florida: Baker County, Hale 21968. Mexico: Chiapas, Hale 20028 (S, US), 20120, 20393, 20445. Panama: Panama, Hale 38446, 38447. Jamaica: Culberson 13748 (DUKE), Plitt (US). Colombia: Lindig 701 (BM, P). Venezuela: Federal, Oberwinkler and Poelt (M, US); Mérida, Hale 42070, 43386; Merinda, Vareschi 2895c (US). Brazil: Rio de Janeiro, Eiten 6541, 7175B, 7674 (US), Glaziov 2000 (UPS); Minas Gerais, Vainio 1589 (TUR, UPS); Rio Grande do Sul.

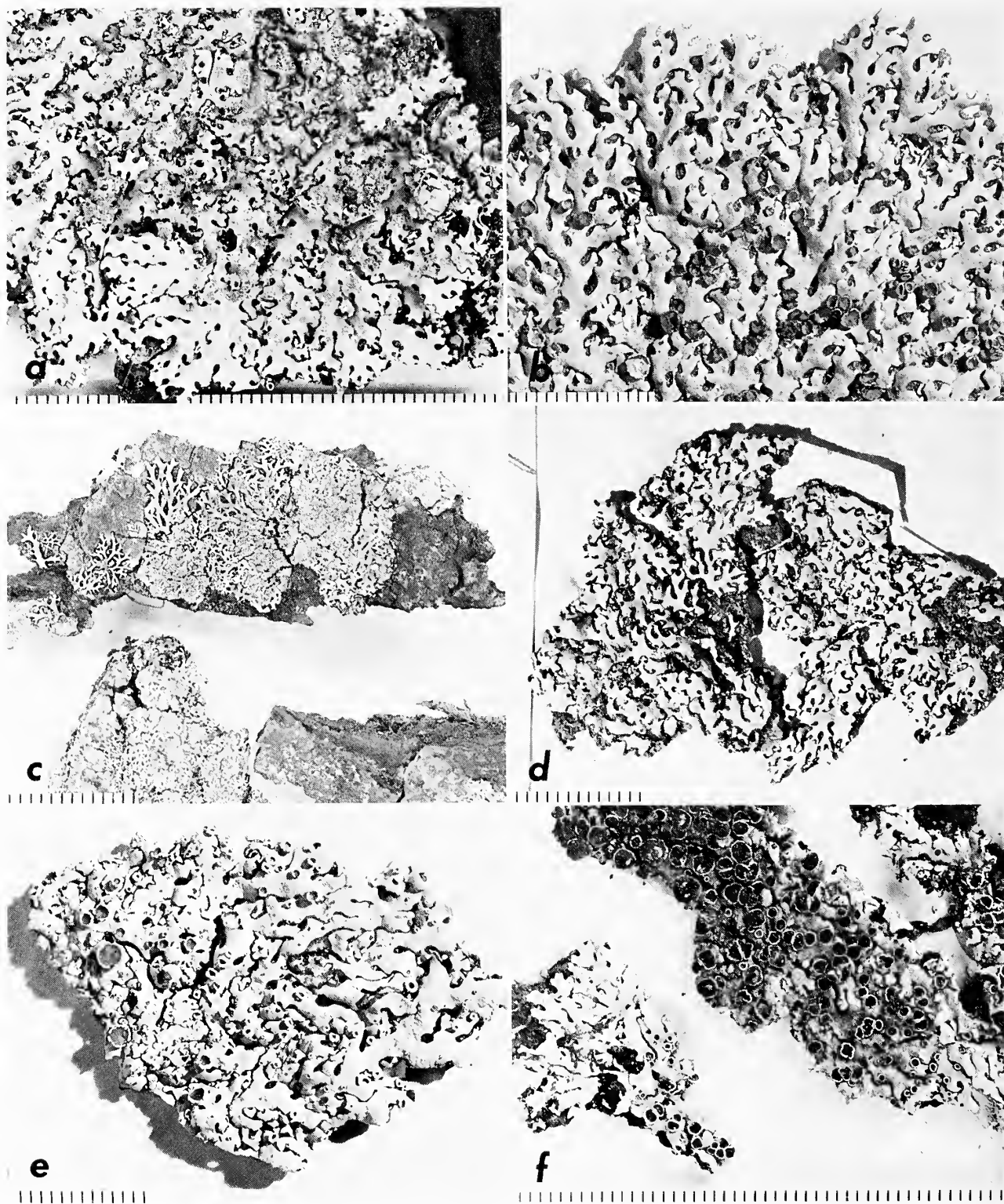


FIGURE 13.—Species of *Relicina*: a, *R. abstrusa* (Hale 20393); b, *R. acrobotrys* (Neervoort 60 pp.); c, *R. amphithrix* (Hale 30051); d, *R. circumnodata* (Maingay in BM); e, *R. connivens* (Hoogland 4726); f, *R. echinocarpa* (Hale 29626). (Scale in mm.)

Rambo 52, 91 (US); Mato Grosso, *Malme* 1481B (S), 1537 (S), 1857 (BM, S), 1865B (S), 1884 (S, W), 2745 (S), 2749B (S), in *Lichenes austroamericani* 94 (G, H, UPS), 95 (G, H, LD, S, UPS, US). Paraguay: Paraguari, *Malme* 1537 (S, US). Argentina: Misiones, *Osorio* 4666 (WIS). Japan: Hyuga, *Hale* 29617, 29646, 29647, 29667; Kii, *Kurokawa* 59085 (TNS, US). Philippines: Mountain, *Hale* 25769, 25818, 25828, 25881, 25888; Cagayan, *Hale* 25625, 25645, 25674, 25675, 25734; Negros Occidental, *Hale* 26432. Malaya: Pahang, *Hale* 30090, 30148, 30149; Selangor, *Hale* 29927, 30058, 30059, 30072, 30090, 20149, 30296, 20397, 30298. Sarawak: *Hale* 29993. Java: *Groenhart* 5868 (US), *Neervoort* 4110 (BO). See *Kurokawa* (1965: 265) for records for Taiwan.

2. *Relicina acrobotrys*

FIGURE 13b

Relicina acrobotrys (Kurokawa) Hale, 1974:484.

Parmelia acrobotrys Kurokawa in Hale and Kurokawa, 1964: 142 [type-collection: Tjibodas, Java, *Neervoort* 60 pr. p. (BO, holotype; US, isotype)].

Thallus adnate on bark, rather coriaceous, 6–12 cm in diameter; lobes sublinear-elongate, 1–2.5 mm wide, narrowly black rimmed; bulbate cilia tapered, not strongly inflated; upper surface plane or rugulose, continuous; lower surface black, densely rhizinate except for a narrow brown zone near the tips, the rhizines black, irregularly densely branched (Figure 8d). Apothecia numerous (frequency 100%), adnate, 1–2.5 mm in diameter, ecoronate, with basal retrorse rhizines; spores 8, 2–3 × 4–6 μ m.

CHEMISTRY.—Medulla K+ yellow turning red, C–, KC– or KC+ orange, P–, atranorin, usnic, consalazinic, and salacinic acids with or without barbatic acid and 4-O-demethylbarbatic acid.

HABITATS.—On trunk and branches of *Quercus* in open forests at 1400–1600 m elevation.

DISTRIBUTION.—Java and Sabah.

REMARKS.—This is the only species with bushy agglutinated rhizines that occurs at high elevation. It is also the only species in *Relicina* with salazinic acid as the main chemical component. While the type contains only salazinic acid, specimens collected later in Sabah all contain barbatic acid in addition. Barbatic acid is also produced in trace amounts by *R. abstrusa* and *R. incongrua*, but these New World populations have no relationship whatsoever to *R. acrobotrys*.

SPECIMENS EXAMINED.—Sabah: *Hale* 28126, 28540, 29123. Indonesia: Java, *Kurokawa* 2167 (TNS, US).

3. *Relicina amphithrix*, new species

FIGURE 13c

Thallus appressus, corticola, viridi-flavicans, 2–6 cm diametro, lobis sublinearibus, angustis, 0.3–1.0 mm latis, margine lobulascentibus, lobulis raro palmato-dactyloideis, bulbo-ciliatis, bulbis inflatis, congestis, acetate apice ramosis, superne dense isidiatis, isidiis cylindricis, cylindricis vel sparse ramosis, pro parte isidiato-lobulascentibus; cortex superior 8–10 μ m crassus, stratum gonidiale 10 μ m crassum, medulla 30–40 μ m crassa, cortex inferior 9–10 μ m crassus (Figure 1f); subtus niger, dense rhizinosus, rhizinis nigris, nitidis, simplicibus vel sparse ramosis. Apothecia rara, adnata, usque ad 1 mm diametro, amphithecio coronato, basin retrorso-rhizinato, disco imperforator, hymenio 30–40 μ m alto, sporis octonis, 3 × 4 μ m.

CHEMISTRY.—Medulla K–, C+, KC+ reddish, P+ red or medulla not reacting with color tests, usnic and echinocarpic acids and associated unknown substances or only usnic acid present.

HOLOTYPE.—Oak forest, elevation about 1600 m, Cameron Highlands, Pahang, Malaya, *M. E. Hale* 30203, 2 March 1965 (US).

REMARKS.—This is the most variable species in *Relicina* and may well represent more than one species. The typical material is clearly isidiate, but the isidia may become procumbent or lobulate. In the extreme case the lobules are far more numerous than isidia over the thallus surface. Intergradation with *R. schizospatha* is a distinct possibility although the two species are fairly easily separated on thallus size and lobe width. A small group of specimens has closely appressed, mostly marginal palmately branched lobules (Figure 1c) often occurring without isidia but seeming to originate from or to intergrade with isidia when isidia are present.

Relicina amphithrix is probably related to *R. relicinula* since both have very narrow lobes and coronate apothecia. *Relicina relicinula*, however, does not produce echinocarpic acid and would therefore differ from the bulk of the specimens identified as *R. amphithrix*. On the other hand, it seems probable that the acid deficient population of *R. amphithrix* is the isidiate morph of *R. relicinula*.

SPECIMENS EXAMINED (echinocarpic acid present, isidiate or becoming lobulate-isidiate).—Philippines: Mountain, *Hale*

25824; Negros Occidental, *Hale* 26420, 26437, 26445, 26480, 26481, 26522, 26569, 26630, 26654; Agusan, *Hale* 24481, 25064, 25191; Surigao del Sur, *Hale* 24674. Malaya: Pahang, *Hale* 30204, 30211, 30479, 20493; Selangor, *Hale* 30066, 30070. Sabah: *Hale* 28239, 28820, 29076.

SPECIMENS EXAMINED (echinocarpic acid, marginally palmate-lobulate).—Philippines: Mountain, *Hale* 25770, 25789; Agusan, *Hale* 24462. Malaya: Selangor, *Hale* 30060, 30063, 30256, 30257, 30258, 30259, 30265, 30283, 30287, 31185, 31186.

SPECIMENS EXAMINED (echinocarpic acid absent, isidiate or becoming lobulate isidiate).—Philippines: Agusan, *Hale* 24454. Malaya: Selangor, *Hale* 30051, 30064, 30065, 30069, 30071, 30288.

4. *Relicina circumnodata*

FIGURE 13d

Relicina circumnodata (Nylander) Hale, 1974:484.

Parmelia circumnodata Nylander in Crombie, 1883:51 [type-collection: Government Hill, Penang, Malaya, *Maingay* 22 (BM, lectotype; FH, H, isolectotypes)].

Thallus closely adnate on bark, 3–8 cm in diameter; lobes sublinear-elongate, 0.7–2 mm wide; bulbate cilia dense and conspicuous, strongly inflated and becoming globose and apically densely branched; upper surface plane to convex, continuous or faintly maculate, sparsely isidiate, the isidia simple, to 0.5 mm high; lower surface pale brown, rhizinate, the rhizines pale, more or less densely branched and agglutinated. Apothecia rare (frequency 10%), adnate, 1–2 mm in diameter, rim coronate; spores 8, cornute, $3 \times 10\text{--}12\ \mu\text{m}$.

CHEMISTRY.—Medulla K—, C—, KC— or KC+ rose, P+ red, protocetraric and usnic acids.

HABITATS.—On trunks and canopy branches of dipterocarp and other trees in rain forest at sea level to 1300 m elevation.

DISTRIBUTION.—Malaya, Philippines, Sarawak.

REMARKS.—This species was described by Nylander from sterile material. Apothecia are now known from 4 of 39 specimens that I have been able to examine. All are coronate and have unusual bicornute spores, exactly the same as those in the presumptive parent species *R. precircumnodata*. The bulbate cilia are very large, globose, and crowded on older parts of the lobes, also as in the parent species. The lower surface is consistently pale brown and the rhizines initially simple but soon branching in the peculiar bushy manner of this group.

The species is very common throughout the

Philippines, northern Borneo, and Malaya. It has not yet been collected south of this region in Indonesia but probably occurs there as well.

SPECIMENS EXAMINED.—Philippines: Mountain, *Hale* 25787, 25802, 25810, 25820, 25841, 25873, 25902; Cagayan, *Hale* 24410, 25736; Quezon, *Hale* 26878, 26879, 26887, 26900, 26920, 26923, 26925, 26928, 26934, 26980; Negros Occidental, *Hale* 26421, 26433, 26474, 26500, 26517, 26561, 26572, 26580, 26599, 26631, 26633, 26651, 26652. Malaya: Pahang, *Hale* 30144; Selangor, *Hale* 30056. Sarawak: *Hale* 29995, 29996, 29997, 29999, 30437.

5. *Relicina connivens*

FIGURE 13e

Relicina connivens (Kurokawa) Hale, 1974:484.

Parmelia connivens Kurokawa in Hale and Kurokawa, 1964: 142 [type collection: Milne Bay district, Papua, New Guinea, *Hoogland* 4726 (BM, holotype; L, US, isotypes)].

Thallus adnate on bark, coriaceous, 3–10 cm in diameter; lobes sublinear-elongate, 1–3 mm wide; upper surface plane to convex, becoming rugulose, continuous to faintly maculate; bulbate cilia large, becoming globose; lower surface black, densely rhizinate, the rhizines black, simple to irregularly densely branched. Apothecia common (frequency 86%), adnate, 1–2.5 mm in diameter, the rim ecoronate, the base retrorsely rhizinate; spores 8, $2\text{--}3 \times 4\text{--}6\ \mu\text{m}$.

CHEMISTRY.—Medulla K—, C—, KC—, P—, protolichestic and usnic acids.

HABITATS.—On trunk and canopy branches of dipterocarps in rain forest and on other trees in secondary forest at 200–850 m elevation.

DISTRIBUTION.—Philippines, Indonesia, New Guinea, Guam, and the Solomon Islands.

REMARKS.—This species has proved to be widespread but not common in a band from the Philippines through New Guinea to the Solomon Islands, occurring generally at 300–800 m elevation. No other species in the genus produces protolichestic acid. It probably would be mistaken for *R. malesiana* (P+ red) without appropriate chemical testing. Closely related *R. subconnivens* has coronate apothecia but if collected sterile it could be differentiated by the presence of caperatic acid.

SPECIMENS EXAMINED.—Philippines: Negros Occidental, *Hale* 26457, 26509, 26626a; Agusan, *Hale*, 25025, 25034, 25044. Solomon Islands: Guadalcanal, *Hill* 9057 (BM, US). Addi-

tional records from the Molucca Islands and Guam are listed in Hale and Kurokawa (1964:143).

6. *Relicina echinocarpa*

FIGURE 13f

Relicina echinocarpa (Kurokawa) Hale, 1974:484.

Parmelia echinocarpa Kurokawa, 1965:265 [type-collection: Mt. Hikosan, Prov. Buzen, Japan, Kurokawa 63163 (TNS, holotype)].

Thallus adnate, to appressed, corticolous or saxicolous, 2–6 cm in diameter; lobes sublinear-elongate, 1–2 mm wide; bulbate cilia gradually inflated; upper surface plane, faintly maculate; lower surface black, densely rhizinate, the rhizines simple or sparsely branched. Apothecia numerous (frequency 100%), adnate, ecoronate, 1–2.5 mm in diameter, with basal retrorse rhizines; spores 8, 3–5 × 6–8 μ m.

CHEMISTRY.—Medulla K+ yellow, C– or C+ pale yellow, KC–, P+ orange, echinocarpic and usnic acids and a C+ unknown with or without salazinic acid.

HABITATS.—On trunk and canopy branches, more rarely on rocks, in open deciduous forest at low elevation.

DISTRIBUTION.—Japan.

REMARKS.—*Relicina echinocarpa* is a small, closely adnate species collected on upper branches of deciduous trees or on rocks in southern Japan, where it appears to be endemic. While it usually contains echinocarpic acid, it is not related to the tropical members of the genus containing this acid. For example, *R. samoensis* has more globose bulbate and coronate apothecia.

The chemical variation in *R. echinocarpa* follows a typical addition pattern. Specimens may contain echinocarpic acid alone, echinocarpic and salazinic acids together, and in one or two specimens apparently salazinic acid alone.

SPECIMENS EXAMINED.—Japan: Hyuga, Hale 29596, 29613, 29626, 29638, 29648, 29658, 29659; Higo, Mayebaru (TNS).

7. *Relicina eximbricata*

FIGURE 14a

Relicina eximbricata (Gyelnik) Hale, 1974:484.

Parmelia samoensis Zahlbruckner var. *eximbricata* Gyelnik,

1938:288 [type-collection: Monte Rus, Cuba, Hioram 10506 (BP, holotype)].

Parmelia eximbricata (Gyelnik) Hale and Kurokawa, 1964:143.

Thallus closely adnate on twigs or bark, 3–5 cm broad; lobes sublinear, 0.7–1.5 mm wide; upper surface plane and continuous; lower surface black, densely rhizinate, the rhizines simple. Apothecia very common (frequency 100%), adnate, 0.5–1.5 mm in diameter, the exciple coronate, the base often retrorsely rhizinate; spores 8, 4–5 × 6–9 μ m.

CHEMISTRY.—Medulla K–, C–, KC–, P+ brick red, fumarprotocetraric, succinprotocetraric, and usnic acids.

HABITATS.—Trunks and branches of trees (cashew, *Eugenia*) in open areas from sea level to 600 m elevation.

DISTRIBUTION.—Florida and the West Indies.

REMARKS.—*Relicina eximbricata* has been collected for the most part in disturbed secondary forest. It is rather rare if the few collections available reflect its true abundance. I was unable, for example, to recollect any specimens at the locality in Florida visited by Swanson. It is extremely close to *R. relicinella* in external appearance but differs in spore number (8 versus 16–32) and presence of succinprotocetraric acid.

SPECIMENS EXAMINED.—See Hale & Kurokawa (1964:144) for specimens from Florida, Cuba, Grand Cayman, Jamaica, and the Dominican Republic.

8. *Relicina fluorescens*

FIGURE 14b

Relicina fluorescens (Hale) Hale, 1974:484.

Parmelia fluorescens Hale, 1965:202 [type-collection: between Kambaranga and the second radio tower, Tourist Trail, Kinabalu National Park, Sabah, Hale 28637 (US, holotype; TNS, isotype)].

Thallus loosely attached to adnate, coriaceous, corticolous, 4–7 cm broad; lobes sublinear-elongate, 1–3 mm wide; bulbate cilia tapered, not strongly inflated; upper surface plane to rugulose and finely pitted, faintly maculate; upper cortex strongly columnar (Figure 5a); surface black, densely rhizinate, the rhizines simple to sparsely branched. Apothecia common (frequency 50%), adnate, 2–3 mm in diameter, ecoronate, usually with basal retrorse rhizines; spores 8, 4 × 5 μ m.

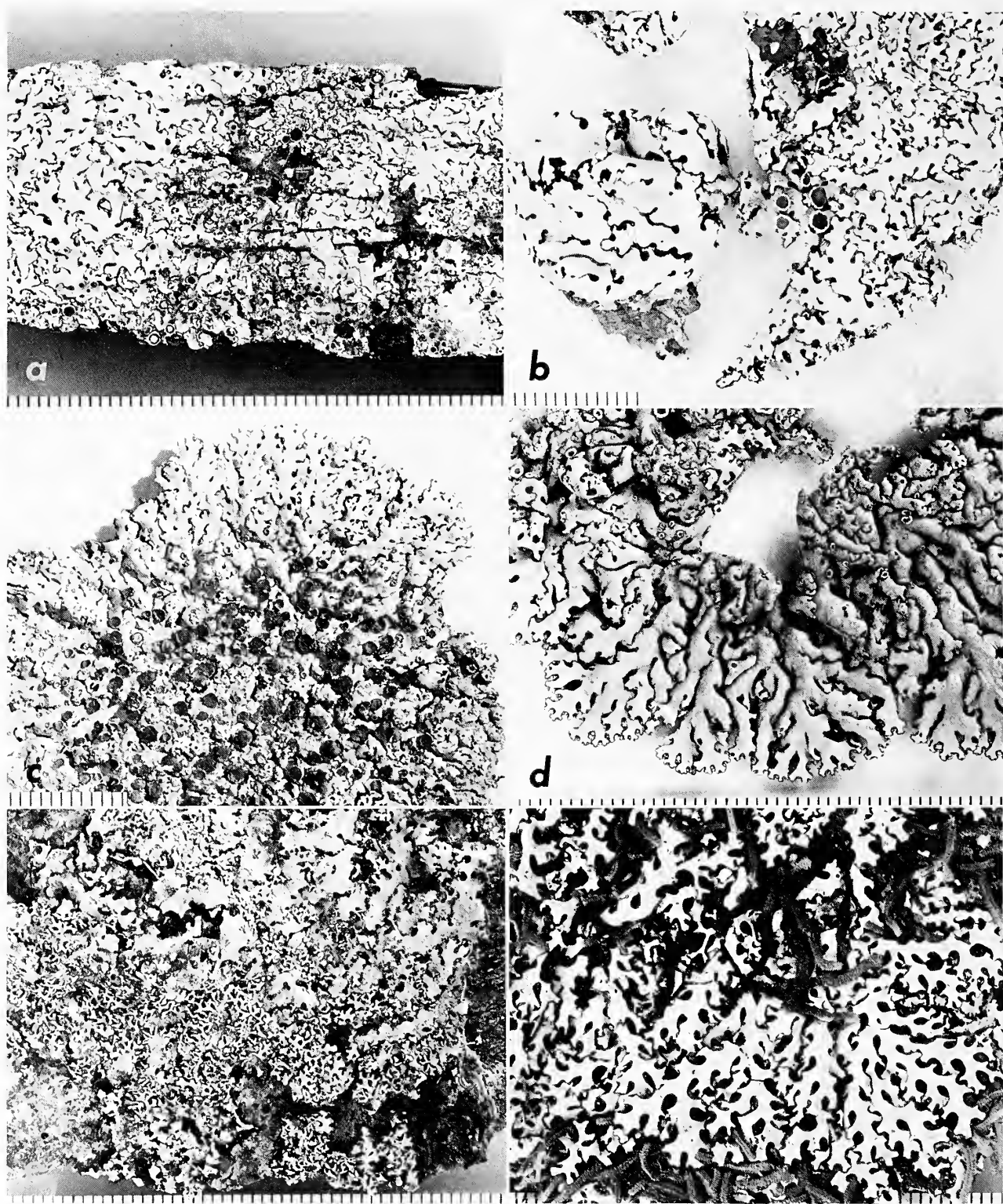


FIGURE 14.—Species of *Relicina*: a, *R. eximbricata* (Imshaug 24518); b, *R. fluorescens* (Hale 29088); c, *R. incongrua* (Malme 2433C); d, *R. limbata* (Du Rietz 4025); e, *R. luteoviridis* (Hale 29069); f, *R. malesiana* (Royen 6232). (Scale in mm.)

CHEMISTRY.—Medulla K—, C—, KC+ rose, or P— or P+ usnic and alectoronic acids with or without echinocarpic acid or echinocarpic acid alone in the medulla.

HABITATS.—On trunk and branches of *Quercus* and other trees in open forest at 1600 to 2400 m elevation.

DISTRIBUTION.—Sabah and New Guinea.

REMARKS.—*Relicina fluorescens* was first recognized by the presence of alectoronic acid. On later study I decided to lump here a series of chemically variable specimens occurring at high elevation, mostly in Sabah. All have coriaceous thalli and a columnar cortex. Once again the primary substance is echinocarpic acid with or without alectoronic acid, but a sizeable part of the population may lack echinocarpic acid. The unknown substance occurring with alectoronic acid in four specimens listed below has an R_F of about 0.25 in the hexane solvent and about 0.6 in the benzene solvent. It is brownish when developed with sulfuric acid. α -Collatolic acid does not occur in this species.

The isidiate morph of *R. fluorescens* is *R. planiuscula*, which has a broader geographic range.

SPECIMENS EXAMINED (alectoronic acid present).—New Guinea, Western Highland: Kurokawa 75 in *Lichenes Rariores et Critici Exsiccati* (US). See Hale (1965: 203) for additional records from Sabah.

SPECIMENS EXAMINED (alectoronic and echinocarpic acids present).—Sabah: Hale 28510, 28512, 29048, 29248.

SPECIMENS EXAMINED (echinocarpic acid present).—Sabah: Hale 28703, 28941, 29088.

SPECIMENS EXAMINED (alectoronic acid and an unidentified substance).—Sabah: Hale 28322, 28750, 29031, 29053.

9. *Relicina incongrua*, new species

FIGURE 14c

Thallus adnatus vel appressus, corticola, viridiflavicans, circa 6 cm diametro, lobis sublinearibus, contiguis, 0.7–1.5 mm latis, margine modice bulbato-ciliatis, bulbis aetate inflatis globosisque; cortex superior circa 10 μ m crassus, stratum gonidiale 10–12 μ m crassum, medulla 70–80 μ m crassa, cortex inferior 10–12 μ m crassis (Figure 2c); subtus niger, modice vel dense rhizinosus, rhizinis nigris, nitidis, simplicibus vel sparse ramosis. Apothecia numerosa (frequentia 100%), adnata, usque ad 2 mm diametro, amphithecio coronato, basin

retorso-rhizinato, hymenio 45–55 μ m alto, sporis octonis, 4–5 \times 5–7 μ m.

CHEMISTRY.—Medulla K—, C—, KC—, KC+, P—, usnic, diffractaic, barbatic, and 4-0-demethylbarbatic acids.

HOLOTYPE.—Santa Anna da Chapada, Mato Grosso, Brazil, Malme 2433C, 27 February 1894 (S; isotype in US).

HABITAT.—On trees in primary forests at low to mid elevation.

DISTRIBUTION.—Panama and Brazil.

REMARKS.—This rare species is externally identical with *R. subabstrusa*, which contains norstictic and salazinic acids. Since this seems to represent a replacement type of chemical population, I am considering it as a distinct species, very closely related to *R. subabstrusa* and probably derived with it from a common progenitor. Both of these species have unfortunately been only rarely collected in tropical America.

SPECIMENS EXAMINED.—Panama: Canal Zone, Hale 43448. Brazil: Mato Grosso, Malme 2445 (S, US).

10. *Relicina limbata*

FIGURE 14d

Relicina limbata (Laurer) Hale, 1974:484.

Parmelia limbata Laurer, 1827:39 [type-collection: Australia, Sieber (M, lectotype)].

Parmelia sphaerospora Knight, 1882:49 [type-collection: Sydney, Australia, Knight (H, lectotype) (not *Parmelia sphaerospora* Nylander, 1859:254)].

Parmelia insinuata Nylander, 1886:324 [based on *Parmelia sphaerospora* Knight].

Thallus adnate to loosely attached on bark or rock, coriaceous, 4–9 cm in diameter; lobes sublinear-elongate, 0.8–2.5 mm wide; bulbate cilia conspicuous, up to 2.5 mm long; upper surface plane to convex, maculate, cracked on older lobes; lower surface brown to blackish brown, moderately rhizinate, the rhizines pale brown, coarse, mostly simple (Figure 8b). Apothecia very common (frequency 100%), adnate, 1–6 mm in diameter, ecoronate, basally retrorsely rhizinate; spores 8, 4–6 \times 7–10 μ m.

CHEMISTRY.—Medulla K+ yellow, C—, KC—. P+ pale orange, norstictic, stictic, and usnic acids with or without atranorin.

HABITAT.—On rocks (granite, sandstone), rarely on trees, in open forests at low elevation.

DISTRIBUTION.—Australia and Tasmania.

REMARKS.—This well-known lichen has been collected only in eastern Australia and Tasmania, where it appears to be common. It was elegantly illustrated in color by Laurer (1827), yet Knight, not apparently having seen Laurer's publication, described it as a new species, *Parmelia sphaerospora*. Knight then sent a specimen to Nylander, who immediately published a new name, *P. insinuata*, since Knight's epithet was a homonym of Nylander's own *P. sphaerospora* published in 1859.

Vainio (1890) comprehended the species correctly, but Asahina's (1934) reports from Japan are *Relicina sydneyensis*, the isidiate morph of *R. limbata*.

SPECIMENS EXAMINED.—Australia: Queensland, *Bailey* 165 (BM), *Hartmann* (US); New South Wales, *Chase* (US), *Du Rietz* 60b, 4025 (UPS, US), *Home* (BM), *Moore* in *Kryptogamae Vindobonensis Exsiccatae* 570 (BM, H, LD, NY, UPS, US), *Weber and McVean* 47322, 49914 (COLO, US), *Wilson* (TNS), in *Lichenes Rariores Exsiccati* 34 (BPI, NY); Tasmania, *Brown* (BM), *Degelius* A-368 (US).

11. *Relicina luteoviridis*

FIGURE 14e

Relicina luteoviridis (Kurokawa) Hale, 1974:484.

Parmelia luteoviridis Kurokawa in Hale and Kurokawa, 1964: 144 [type-collection: B. Papan, Beu territory, E. Kutai, Borneo, *Meijer* B1948 (BO, holotype; US, isotype)].

Thallus adnate on bark, fragile, 5–8 cm in diameter; lobes sublinear-elongate, 1.5–3 mm wide; upper surface plane, faintly maculate, lobulate, the lobules large, dorsiventral, marginally bulbate-ciliate, procumbent, often dichotomously branched (Figure 14e); cortex columnar (Figure 5b); bulbate cilia long and tapered; lower surface black, densely rhizinate, the rhizines black, simple or sparsely branched. Apothecia not seen.

CHEMISTRY.—Medulla K–, C+ rose, KC+ red, P–, gyrophoric and usnic acids with or without atranorin.

HABITATS.—On upper branches of evergreen trees in rain forest at 600–1400 m elevation.

DISTRIBUTION.—Sabah.

REMARKS.—*Relicina luteoviridis* can be recognized by the large lobules and the unique chemistry. It is the only species containing gyrophoric acid. Only three collections are known, all from Borneo.

SPECIMENS EXAMINED.—Sabah: *Hale* 29069, *Meijer* B548a (BO, US).

12. *Relicina malesiana*

FIGURE 14f

Relicina malesiana (Hale) Hale, 1974:484.

Parmelia malesiana Hale, 1965:203 [type-collection: Florida logging area, about 30 km southeast of Butuan City, Agusan Prov., Philippines, *Hale* 25370 (US, holotype; TNS, UPS, isotypes)].

Thallus adnate on bark, 6–8 cm broad; lobes sublinear-elongate, 1.5–2.5 mm wide; bulbate cilia gradually inflated; upper surface plane to rugulose, faintly maculate; medulla white, very rarely in part orange red; lower surface dark brown or blackening, densely rhizinate, the rhizines black, simple to squarrosely branched. Apothecia numerous (frequency 80%), adnate, ecoronate; spores 8, 2–4 × 3–7 μm, medulla below the hymenium rarely orange red.

CHEMISTRY.—Medulla K–, C–, KC–, P+ red, usnic and fumarprotocetraric acids and if pigmented an unidentified K+ purple anthraquinone.

HABITAT.—On trunk and branches of dipterocarps and other trees in rain forest at 150–600 m elevation.

DISTRIBUTION.—Taiwan, Philippines, Sabah, and New Guinea.

REMARKS.—The lower surface of this species is generally black but may be in part dark brown. The rhizines when fully branched appear to be squarrose, black, rather thin, and shiny. It is somewhat related, then, to species like *R. ramosissima*, which has a consistently pale brown lower surface and pale agglutinated rhizines, succinprotocetraric acid in addition to fumarprotocetraric acid, and smaller spores. It is also chemically related to *R. sublimbata*, which contains both fumarprotocetraric and succinprotocetraric acids.

SPECIMENS EXAMINED.—New Guinea: Hollandia, *Royen and Sleumer* 6232 (L, US). See Hale (1965:203) for additional records for Taiwan, Philippines, and Sabah.

13. *Relicina planiuscula*

FIGURE 15a

Relicina planiuscula (Kurokawa) Hale, 1974:484.

Parmelia planiuscula Kurokawa in Hale and Kurokawa, 1964:

144 [type-collection: Kandang Badak, Java, *Neervoort* 427 (BO, holotype; US, isotype)].

Thallus adnate on bark, coriaceous, 5–9 cm in diameter; lobes sublinear-elongate, 1–3 mm wide; upper surface plane, faintly maculate, sparsely to moderately isidiate, the isidia simple, less than 0.7 mm high, frequently procumbent, rarely lobulate; upper cortex strongly columnar (Figure 5c); lower surface black, moderately rhizinate, the rhizines simple, black. Apothecia rare (frequency 11%), adnate, 1–2 mm in diameter, ecoronate, the amphithecium isidiate; spores 8, $4 \times 5 \mu\text{m}$.

CHEMISTRY.—Medulla K+ yellowish, C+ faint yellow orange, KC–, P+ yellow, echinocarpic and usnic acids and a C+ unknown with or without atranorin.

HABITATS.—On trunk and branches of *Quercus*, *Pinus*, and other trees in open forests and mossy forest at 1500–2200 m (at lower elevation in Japan and Taiwan).

DISTRIBUTION.—Japan, Taiwan, Philippines, Malaya, Indonesia, and Sabah.

REMARKS.—This is the commonest species of *Relicina* at higher elevations in Southeast Asia. The presumptive parent of this isidiate morph is *R. fluorescens*, which has a much more restricted distribution. While most specimens have sparse to moderate development of cylindrical isidia, others have procumbent lobulate isidia. The population on *Pinus* in the northern Philippines is especially strongly isidiate-lobulate, and I had at first considered it to be a separate species.

SPECIMENS EXAMINED.—Japan, Hyuga: *Hale* 29665. Philippines: Mountain, *Hale* 26088, 26089, 26102, 26113, 26117, 26173, 26195, 26806. Malaya: Pahang, *Hale* 29929, 29943, 29944, 29945, 29946, 29949, 30481, 30497. Sabah: *Hale* 28006, 28040, 28063, 28234, 28250, 28257, 28372, 28400, 28508, 28546, 28580, 28581, 28603, 28700, 28815, 29035, 29168, 29250. Indonesia: Java, *Groenhart* 2217 (L); Sumatra, *Steenis* 1895 (BO).

14. *Relicina precircumnodata*, new species

FIGURE 15b

Thallus adnatus, corticola, viridi-flavicans, 4–10 cm diametro, lobis sublinearibus, contiguus vel separatis, 1–2 mm latis, margine dense bulbo-ciliatis, bulbis globosis, sorediis isidiisque destitutis; cortex superior circa 12 μm crassus, stratum gonidiale 10

μm crassum, medulla 100–120 μm crassa, cortex inferior circa 12 μm crassus (Figure 2h); subtus pallide castaneus, dense rhizinosus, rhizinis pallidis, dense ramosis atque agglutinatis. Apothecia adnata, usque ad 2 mm diametro, amphithecio crenato, coronato, basin retrorso-rhizinato, hymenio 70–80 μm alto, sporis octonis, bicornutis, $2-3 \times 11-13 \mu\text{m}$.

CHEMISTRY.—Medulla K–, C–, P+ red, protocetraric and usnic acids.

HOLOTYPE.—Virgin dipterocarp forest, Tungao Logging Area, 40 km SE Butuan City, Agusan Province, Philippines, elevation about 400 m, *M. E. Hale* 25044a, July 1964 (US).

HABITATS.—On canopy branches of dipterocarps in rain forest at 100–400 m elevation.

DISTRIBUTION.—Philippines.

REMARKS.—This species represents the presumptive nonisidiate morph of *R. circumnodata*. Both contain protocetraric acid and have unusual bicornute spores. *Relicina precircumnodata* is by far the rarer of this species pair, occurring only at three widely separate localities in the Philippines.

SPECIMENS EXAMINED.—Philippines: Cagayan, *Hale* 24418; Mountain, *Hale* 25826.

15. *Relicina ramosissima*

FIGURE 15c

Relicina ramosissima (Kurokawa) Hale, 1974:485.

Parmelia ramosissima Kurokawa in Hale and Kurokawa, 1964:145 [type-collection: Tenimber Island, Moluccas, *Buwalda* 4583 (BO, holotype; US, isotype)].

Thallus adnate, corticolous, 3–10 cm in diameter; lobes sublinear-elongate, 0.7–2 mm wide; bulbate cilia gradually inflated to gobose, becoming apically branched; upper surface plane, maculate; lower surface pale to dark brown, moderately rhizinate, the rhizines simple to densely branched and agglutinated, pale (Figure 8f). Apothecia common (frequency 93%), adnate, 1–2.5 mm in diameter, ecoronate, often retrorsely rhizinate at the base; spores 8, $2 \times 3 \mu\text{m}$.

CHEMISTRY.—Medulla K–, C–, KC+ reddish, P+ red, usnic acid, fumarprotocetraric acid, and succinprotocetraric acid.

HABITAT.—On trunk and canopy branches of dipterocarps in rain forest at 150–300 m elevation.

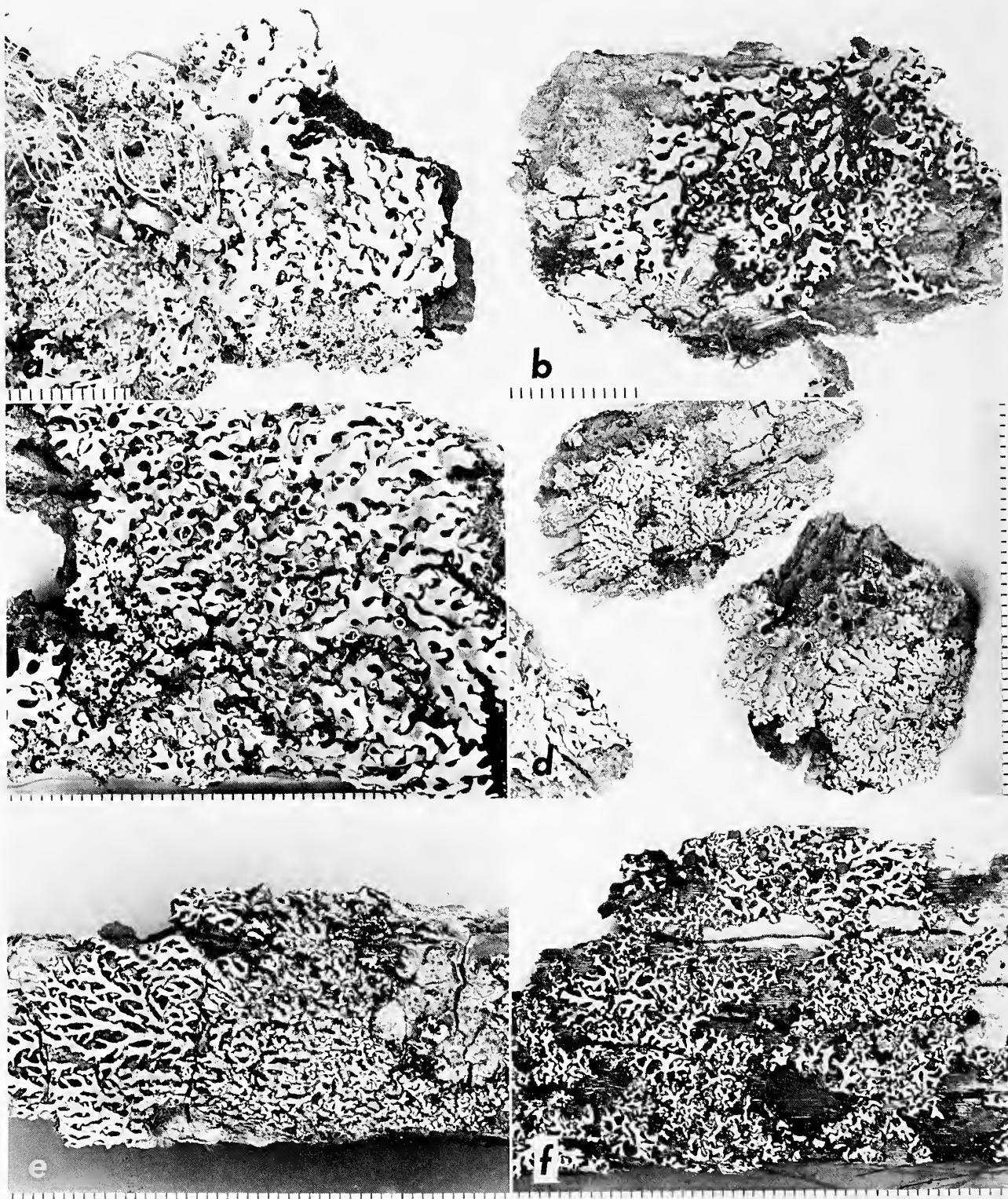


FIGURE 15.—Species of *Relicina*: a, *R. planiuscula* (Hale 26806); b, *R. precircumnodata* (Hale 24418); c, *R. ramosissima* (Hale 29923); d, *R. relicinella* (Nee 3766); e, *R. relicinula* (Hale 24402); f, *R. samoensis* (Hale 26955). (Scale in mm.)

DISTRIBUTION.—Malaya, Philippines, Sabah, and Indonesia.

REMARKS.—This species has a wide distribution in the dipterocarp forests. It superficially resembles *R. sublanea*, which differs in producing protocetraric acid, in having large spores ($4-5 \times 7-9 \mu\text{m}$), and in occurring generally above 300–400 m elevation, higher than *R. ramosissima*.

SPECIMENS EXAMINED.—Philippines: Agusan, *Hale* 25245, 25360. Malaya: Selangor, *Hale* 29923, 30062, 30074, 30075, 30290, 30291, 30300. Sabah: *Hale* 30352, 30355, 30356, 30357, 30366. Indonesia: Java, *Groenhart* 8374 (BO).

16. *Relicina relicinella*

FIGURE 15d

Relicina relicinella (Nylander) Hale, 1974:485.

Parmelia relicinella Nylander 1885:215 [type-collection: Santarem, Brazil, *Spruce* 136 (H, lectotype; BM, G, P, isolectotypes)].

Thallus closely adnate on bark, 3–6 cm in diameter; lobes sublinear, 0.5–1.5 mm wide; bulbate cilia distinct, short; upper surface plane, continuous; lower surface black, densely rhizinate, the rhizines simple or sparsely branched. Apothecia common (frequency 100%), adnate, 0.5–1.5 mm in diameter, the disc concave to plane, the exciple coronate; spores 16–32, $3-4 \times 5-6 \mu\text{m}$.

CHEMISTRY.—Medulla K–, C–, KC–, P+ red, usnic acid, fumarprotocetraric acid, and an unidentified P+ compound.

HABITAT.—On tree trunks and branches in rain forest at 100–200 m elevation.

DISTRIBUTION.—Colombia and Brazil.

REMARKS.—The most unusual feature of this species is the multispored asci, recognized by Nylander (1885) in his original description. It is very similar externally to *R. eximbricata* but seems to occur only in virgin rain forest. It may be a common species in the vast lowland rain forests of South America, but no lichenologists have yet had an opportunity to visit these habitats.

SPECIMENS EXAMINED.—Colombia: Santander, *Nee and Mori* 3766. Brazil: Amazonas, *Spruce* 58 (BM, US).

17. *Relicina relicinula*, new combination

FIGURE 15e

Parmelia relicinula Müller Argau, 1882:317 [type-collection: Java, *Junghuhn* 3728 (G, lectotype)].

Parmelia relicina Fries, 1825:283 [type-collection: *Gaudichaud* 54, Rawak (Pacific area) (UPS, lectotype; P. isolectotype)].

Thallus closely adnate to appressed on bark, 2–6 cm broad; lobes variable, short, contiguous and sublinear to separate and sublinear-elongate, 0.3–1.5 mm wide; bulbate cilia short but conspicuous, strongly inflated, sometimes apically branched; upper surface plane, continuous to faintly maculate, without lobules or becoming marginally lobulate, isidia lacking; lower surface black, densely rhizinate, the rhizines black, simple to sparsely branched. Apothecia very common (frequency 94%), adnate, about 1 mm in diameter, the exciple coronate, the base often retrorsely rhizinate; spores 8, $4-5 \times 5-7 \mu\text{m}$.

CHEMISTRY.—Medulla K–, C–, KC–, P–, usnic acid and unidentified colorless substances.

HABITAT.—On trunk and canopy branches of dipterocarps and other trees in rain forest at 100–400 m elevation.

DISTRIBUTION.—Philippines, Malaya, and Indonesia.

REMARKS.—The characteristic features of this widespread species are the narrow appressed lobes and lack of lichen substances in the medulla. It is an extremely variable species, however, particularly in regard to production of marginal lobes. Some specimens have no obvious lobules. Müller's type-specimen is somewhat lobulate. He described *Parmelia relicinula* as being 2–3 times narrower than *P. relicina* Fries, but I doubt that he saw Fries' type. The excellent material of *P. relicina* in Paris has very narrow lobes. This specimen does lack lobules. Its chemistry is still undecided since, although it is negative with color tests, a dull, high unidentified spot appears on TLC plates. Similar but not identical spots were discovered in several of the Philippine specimens.

Asahina (1934) reported *Parmelia relicina* from southern Japan. I have not seen this material but suspect that it is *Relicina echinocarpa*.

SPECIMENS EXAMINED.—Philippines: Mountain, *Hale* 25849, 25871; Cagayan, *Hale* 24402, 24416, 25604, 25638, 25652, 25657, 25658, 25737; Cavite, *Hale* 26836; Sorsogon, *Elmer* 16031 (F, US); Agusan, *Hale* 24996, 25011, 25659; Surigao del Sur, *Hale* 24641, 24698, 24700; Zamboanga del Sur, *Hale* 24521, 24704, 24709, 24733, 24738, 24748, 24807, 24826, 24827, 24861, 25159, 25313. Malaya: Selangor, *Hale* 29925, 30281. Java: *Groenhart* 1702 (L). Thursday Island: *Hartmann* in *Lichenotheca Universalis* 159 (S, US).

18. *Relicina samoensis*

FIGURE 15f

Relicina samoensis (Zahlbruckner) Hale, 1974:485.

Parmelia samoensis Zahlbruckner, 1908:272 [type-collection: Malifa, Upolu, *Rechinger* 5005 (W, lectotype)].

Thallus adnate to closely adnate, corticolous, 4–8 cm in diameter; lobes rather short, sublinear, 0.3–1 mm wide; bulbate cilia conspicuous, globose, up to 1 mm long; upper surface plane, continuous; lower surface black, densely rhizinate, the rhizines black, simple or sparsely branched. Apothecia adnate, very common (frequency 100%), 1–3 mm in diameter, the exciple coronate, the base retrorsely rhizinate; spores 8, $5\text{--}6 \times 6\text{--}7 \mu\text{m}$.

CHEMISTRY.—Medulla K+ yellow, C+ faint orange, KC–, P+ yellow orange, usnic and echinocarpic acids and a C+ unknown.

HABITAT.—On coconut palm and other trees in disturbed areas at 100–700 m elevation.

DISTRIBUTION.—Philippines, Java, New Caledonia, Samoa, and Society Islands.

REMARKS.—*Relicina samoensis* is a lowland species occurring in secondary forests. The lobes vary considerably in size but are usually narrow and closely adnate. This is the only species with echinocarpic acid that has coronate apothecia.

SPECIMENS EXAMINED.—Philippines: Quezon, *Hale* 26955. Indonesia: Halmahera, *Groenhart* 8343 (BO); Java, *Bredijn* 1099 (BO), *Palmer* 614 (US). Samoa: *Reinecke* 22 p. p. (BO, US). New Caledonia: *Hill* 11590 (BM). Society Islands: *Moore* 13 (US).

19. *Relicina schizospatha*

FIGURE 16a

Relicina schizospatha (Kurokawa) Hale, 1974:485.

Parmelia schizospatha Kurokawa in Hale and Kurokawa, 1964:146 [type-collection: Gegerbentang, Java, *Neervoort* 1062 (BO, holotype; US, isotype)].

Thallus adnate, corticolous, rather fragile, 3–6 cm in diameter; lobes short, sublinear, 1–2 mm wide; bulbate cilia not conspicuous or dense; upper surface plane, faintly maculate, becoming more or less densely lobulate along the margins and surface, the lobules dorsiventral, procumbent to subascending, sometimes dactyloid branched, rarely with marginal bulbils (Figure 16); lower surface

black, moderately rhizinate, the rhizines simple. Apothecia unknown.

CHEMISTRY.—Medulla K– yellow, C– or C+ faint orange, KC–, P+ orange, usnic and echinocarpic acids and a C+ unknown.

HABITAT.—On trunk and branches of *Quercus* and other trees in rain forest at 1300–1600 m elevation.

DISTRIBUTION.—Malaya, Philippines, Sabah, and Indonesia.

REMARKS.—The distinguishing feature of this species is the distinct marginal and laminal lobules (Figure 1b). These lobules are dorsiventral, simple to forked, and sometimes subascending. Bulbate cilia are rarely developed on the margins in contrast, for example, to the abundant production of bulbils in *R. luteoviridis*. There is some intergradation with echinocarpic-acid-containing specimens of *R. amphithrix*, which have strongly lobulate isidia. On the average *R. amphithrix* would have much narrower lobes than *R. schizospatha* and some trace of isidial initials. In addition *R. amphithrix* is rare at the higher elevations where *R. schizospatha* normally occurs. In addition, although *R. schizospatha* is sterile, I suspect that the apothecia, when discovered, will be ecoronate.

SPECIMENS EXAMINED.—Philippines: Bukidnon, *Sulit* 14806 (US). Malaya: Pahang, *Hale* 30089, 30142, 30210, 30216, 30221, 30222, 30223, 30486, 30494. Sabah: *Hale* 28156, 28157, 28221, 29026, 29037, 29117, 29285. Indonesia: Java, *Groenhart* 2219 (L, US), *Ooststroom* 14198, 14300 (L, US). A record from Taiwan by Kurokawa (1965:267), which I have not been allowed to examine, is probably *R. amphithrix*.

20. *Relicina subabstrusa*

FIGURE 16b

Relicina subabstrusa (Gyelnik) Hale, 1974:485.

Parmelia subabstrusa Gyelnik, 1931:288 [based on *P. abstrusa* f. *laevigata* Lyng].

Parmelia limbata f. *endococcinea* Müller Argau, 1887:318 [type-collection: Russell River, Australia, *Sayer* 19 (G, lectotype)].

Parmelia abstrusa f. *laevigata* Lyng, 1914:147 [type-collection: Bocca da Serra, Serra da Chapada, Mato Grosso, Brazil, *Malme* (S, lectotype)].

Parmelia endococcinea (Müller Argau) Gyelnik, 1931:288.

Parmelia decaryana Gyelnik, 1934:153 [type-collection: Tsantsani, Anjouan, Comoro Island, *Decary* (BP, holotype)].

Parmelia kilauae f. *laevigata* (Lyng) Gyelnik, 1935:37.

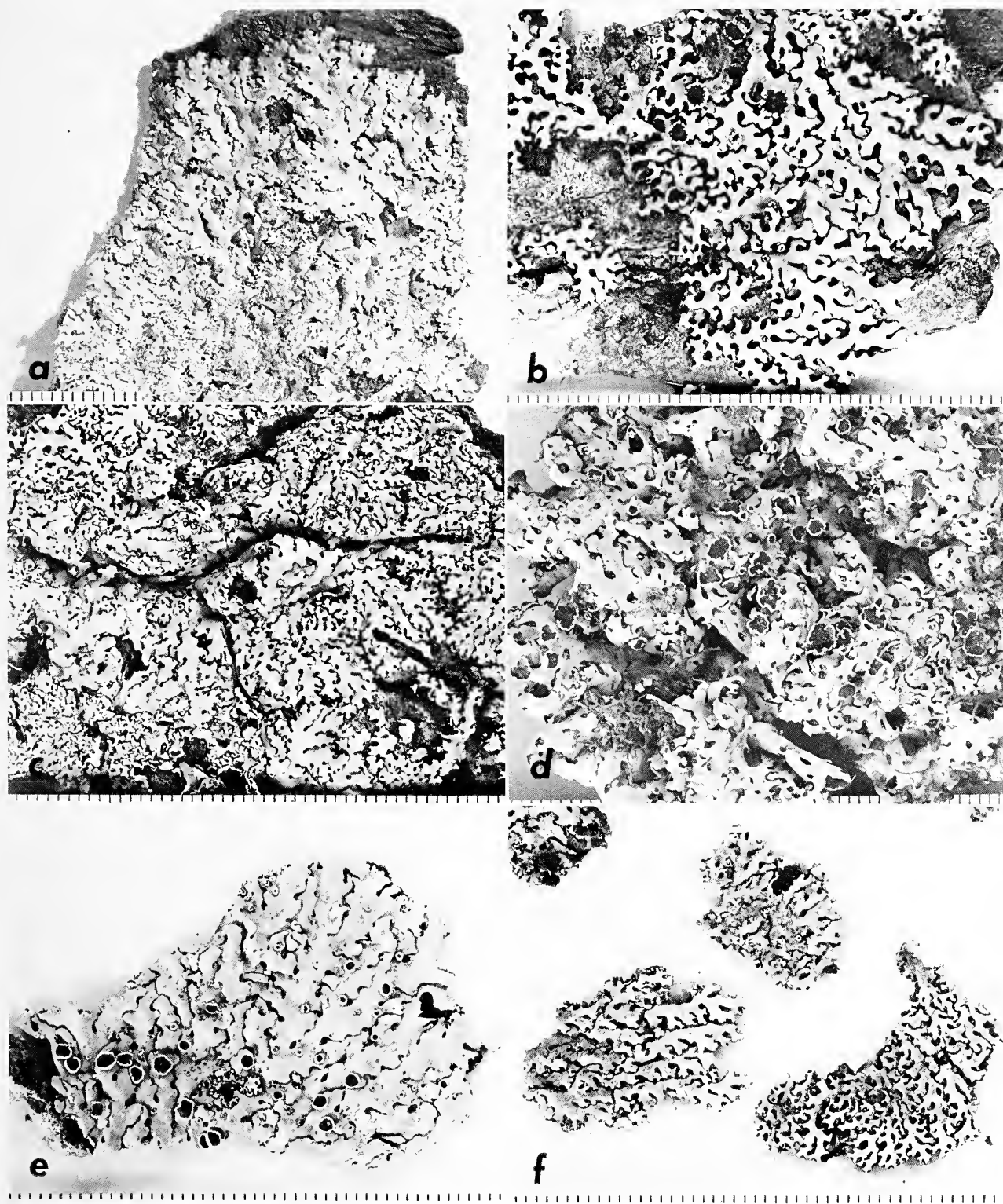


FIGURE 16.—Species of *Relicina*: a, *R. schizospatha* (Neervoort 1062); b, *R. subabstrusa* (Hale 25800); c, *R. subconnivens* (Hale 30054); d, *R. sublanca* (Hale 26650); e, *R. sublimbata* (Kurokawa 1872); f, *R. sydneyensis* (Weber 49048). (Scale in mm.)

Thallus adnate on bark, 4–8 cm broad; lobes sublinear, 0.5–2 mm wide; bulbate cilia numerous, strongly inflated, to 1 mm long; upper surface plane, continuous; lower surface black, densely rhizinate, the rhizines black, simple (Figure 8c). Apothecia very common (frequency 83%), adnate, 1–3 mm in diameter, the exciple strongly coronate; spores 8, $4 \times 7\text{--}8\text{ }\mu\text{m}$.

CHEMISTRY.—Medulla K+ yellow turning red, C–, KC–, P+ orange, norstictic and usnic acids with or without salazinic acid.

HABITAT.—On trunk and branches of dipterocarps in Old World rain forest and in secondary forest at sea level to 850 m elevation and on trees at mid elevations in the New World.

DISTRIBUTION.—Taiwan, Philippines, Sarawak, Australia, Comoro Islands, Brazil, and Paraguay.

REMARKS.—*Relicina subabstrusa* has the broadest geographic range of any species in the genus but is commonly collected only in the Philippines. As with *R. abstrusa*, its presumptive isidiate morph, the Old World population lacks or has only traces of salazinic acid, whereas salazinic is produced in heavy concentration in the New World. Müller's specimen of f. *endococcinea* is red because of the decomposition of norstictic acid.

SPECIMENS EXAMINED.—Philippines: Mountain, *Hale* 25760, 25762, 25772, 25781, 25797, 25800, 25801, 25812, 25817, 25838, 25858, 25863, 25879, 25898, 25901, 25802a, 25913, 26506; Cagayan, *Hale* 25608, 25654, 25661, 25751; Cavite, *Hale* 26811, 26828; Polillo, *Leiberg* 532 (US); Negros Occidental, *Hale* 26427, 26444, 26449, 26473, 26494, 26494a, 26510, 26519, 26564, 26581, 26626, 26632, 26693, 26696; Agusan, *Hale* 24460, 24474, 24984, 25003, 25014, 25029, 25033, 25048; Basilan, *Hale* 24935, 24949, 25141, 25333. Sarawak: *Hale* 29991. Paraguay: *Balansa* (H). See Kurokawa (1965:267) for records from Taiwan.

21. *Relicina subconnivens*, new species

FIGURE 16c

Thallus adnatus, corticola, viridi-flavicans, circa 10 cm latus, lobis sublinearibus, contiguus, sparse lobulatis, margine dense bulbo-ciliatis, bulbis aetate inflatis, globosis, isidiis sorediisque destitutis; cortex superior 10–12 μm crassus, stratum gonidiale circa 12 μm crassum, medulla 60–80 μm crassa, cortex inferior 16–18 μm crassus (Figure 3f); subtus niger, dense rhizinosus, rhizines nigris, nitidis,

simplicibus vel sparse ramosis. Apothecia adnata, 0.5–1.0 mm diametro, amphithecio coronato, basin retrorso-rhizinato, disco carneo, imperforato, sporis octonis, $3 \times 4\text{ }\mu\text{m}$.

CHEMISTRY.—Medulla negative with color tests, usnic and caperatic acids.

HOLOTYPE.—Virgin dipterocarp forest, Ulu Gombak Forest Reserve, 15 km NE of Kuala Lumpur, elevation about 300 m, *M. E. Hale* 30054, 5 March 1965 (US).

REMARKS.—This species was first identified as *R. connivens*. It differs primarily in having coronate apothecia and very small spores and in containing caperatic acid rather than protolichesterinic acid. It is known only from the type collection.

22. *Relicina sublanea*

FIGURE 16d

Relicina sublanea (Kurokawa) Hale, 1974:485.

Parmelia sublanea Kurokawa in Hale and Kurokawa, 1964: 146 [type-collection: Halmahera Island, Indonesia, *Groenhardt* 8409 (BO, holotype; US, isotype)].

Thallus adnate on bark, coriaceous, 6–10 cm in diameter; lobes sublinear-elongate, 1–2 mm wide; bulbate cilia strongly inflated; upper surface more or less convex, continuous; lower surface pale brown, densely rhizinate, the rhizines densely branched, and agglutinated (Figure 8g). Apothecia common (frequency 60%), adnate, 1–4.5 mm in diameter, ecoronate; spores 8, $4\text{--}5 \times 7\text{--}9\text{ }\mu\text{m}$.

CHEMISTRY.—Medulla K–, C–, KC+ rose, P+ orange red, usnic and protocetraric acids.

HABITAT.—On trunk and canopy branches of dipterocarps in rain forest at 300–850 m elevation.

DISTRIBUTION.—Southern Philippines, Malaya, and Indonesia.

REMARKS.—This is another typical dipterocarp forest lichen characterized by pale agglutinated rhizines and protocetraric acid. Its relation to *R. ramosissima* is discussed under that species. The only other nonisidiate species with protocetraric acid, *R. precircumnodata*, has coronate apothecia.

SPECIMENS EXAMINED.—Philippines: Negros Occidental, *Hale* 26459, 26578, 26650, 26657; Surigao del Sur, *Hale* 24635, 24655; Zamboanga del Sur, *Hale* 24793, 25310; Basilan, 24920, 24922. Malaya: Selangor, *Hale* 30280.

23. *Relicina sublimbata*

FIGURE 16e

Relicina sublimbata (Nylander) Hale, 1974:485.

Parmelia sublimbata Nylander, 1885:615 [type-collection: Yomah in Pegu, Burma, Brandis 595 (M, lectotype; H, isolectotype)].

Thallus adnate on bark or rock, coriaceous, 4–8 cm in diameter; lobes sublinear-elongate, 1–2.5 mm wide; bulbate cilia coarse, inflated, to 1 mm long; upper surface plane, continuous; lower surface black, densely rhizinate, the rhizines black, simple to sparsely branched. Apothecia adnate, 1–2 mm in diameter, ecoronate; spores 8, 4–5 × 5–6 μm.

CHEMISTRY.—Medulla K+ reddish, C–, KC–, P+ orange red, usnic acid, fumarprotocetraric acid, and succinprotocetraric acid.

HABITAT.—On tree trunks and rocks at mid elevation (1300–1400 m in Thailand).

DISTRIBUTION.—Burma and Thailand.

REMARKS.—Nylander (1885) separated this species from *R. limbata* because of the smaller spores (4.5 × 6–8 μm) and whitish color. The two species are, in fact, totally unrelated. *Relicina sublimbata* is actually very close to *R. malesiana*, which produces fumarprotocetraric acid alone, has more branched rhizines and smaller spores, and does not occur on mainland Asia. *Relicina sublimbata* seems to be restricted to the Burma-Thailand region but little is known of its full range there.

SPECIMENS EXAMINED.—Thailand: Kurokawa 1872 (TNS, US).

24. *Relicina sydneyensis*

FIGURE 16f

Relicina sydneyensis (Gyelnik) Hale, 1974:485.

Parmelia sydneyensis Gyelnik, 1938:292 [type-collection: Mossman's Bay, Sydney, Australia, Cheel (BP, holotype)].

Parmelia limbata Laurer f. *isidiosa* Müller Argau, 1887:59 [type-collection: Richmond River, Australia, Hodgkinson (G, lectotype)].

Parmelia tumescens Hale and Kurokawa, 1964:147 [based on *P. limbata* f. *isidiosa* Müller Argau].

Parmelia subturgida Kurokawa, 1965:268 [type-collection: Bandagamori, Prov. Tosa, Japan, Makino (TNS, holotype; US, isotype)].

Thallus adnate on bark or rocks, 3–8 cm in diameter; lobes sublinear to sublinear-elongate, contiguous, 0.8–1.5 mm wide; bulbate cilia tapered to strongly inflated; upper surface plane, faintly maculate, irregularly cracked with age, isidiate, the isidia simple, to 0.8 mm high; lower surface brown to dark brown, moderately rhizinate, the rhizines brown or black, mostly simple. Apothecia rare, adnate, 1.5–3.5 mm in diameter, ecoronate, the base retrorsely rhizinate; spores 8, 4–5 × 7–8 μm.

CHEMISTRY.—Medulla K+ yellow turning red, C–, KC–, P+ orange, usnic, norstictic, and stictic acids with or without atranorin.

HABITAT.—On bark of trees and more rarely on rocks in open forests at low elevation.

DISTRIBUTION.—Japan, Taiwan, Java, and Australia.

REMARKS.—Müller Argau recognized the close relation between this and *R. limbata*; *R. sydneyensis* would appear to be the isidiate morph of *R. limbata*. It has identical chemistry but seems to occur more frequently on trees and, of course, to have a broader geographic range. Chromatographic profiles of the types of *Parmelia limbata* f. *isidiosa* and *P. subturgida* are identical. Hale and Kurokawa (1964) proposed the name *Parmelia tumescens* but later discovered that the type of *P. sydneyensis* Gyelnik is actually sparsely isidiate, not nonisidiate.

SPECIMENS EXAMINED.—Japan: Izu, Kurokawa 58622 (US). Indonesia: Java, Nervoort 5874 (BO). Australia: New South Wales, Weber and McVean L-49048 (COLO, US); Queensland, Du Rietz 4234:1 (UPS, US). See Kurokawa (1965:268) for records from Taiwan.

Nomen Inquirendum: *Parmelia nigrociliata*

Parmelia nigrociliata Hillmann, 1940:39 [type-collection: Mutautu, Samoa, Vaupel (destroyed at B); (not *Parmelia nigrociliata* Bouly de Lesdain ex anno 1933)].

This species cannot be typified since the type (and only known) collection was lost at Berlin. The description and remarks by Hillmann, however, leave little doubt that it is synonymous with *Relicina samoensis* (Zahlbruckner) Hale.

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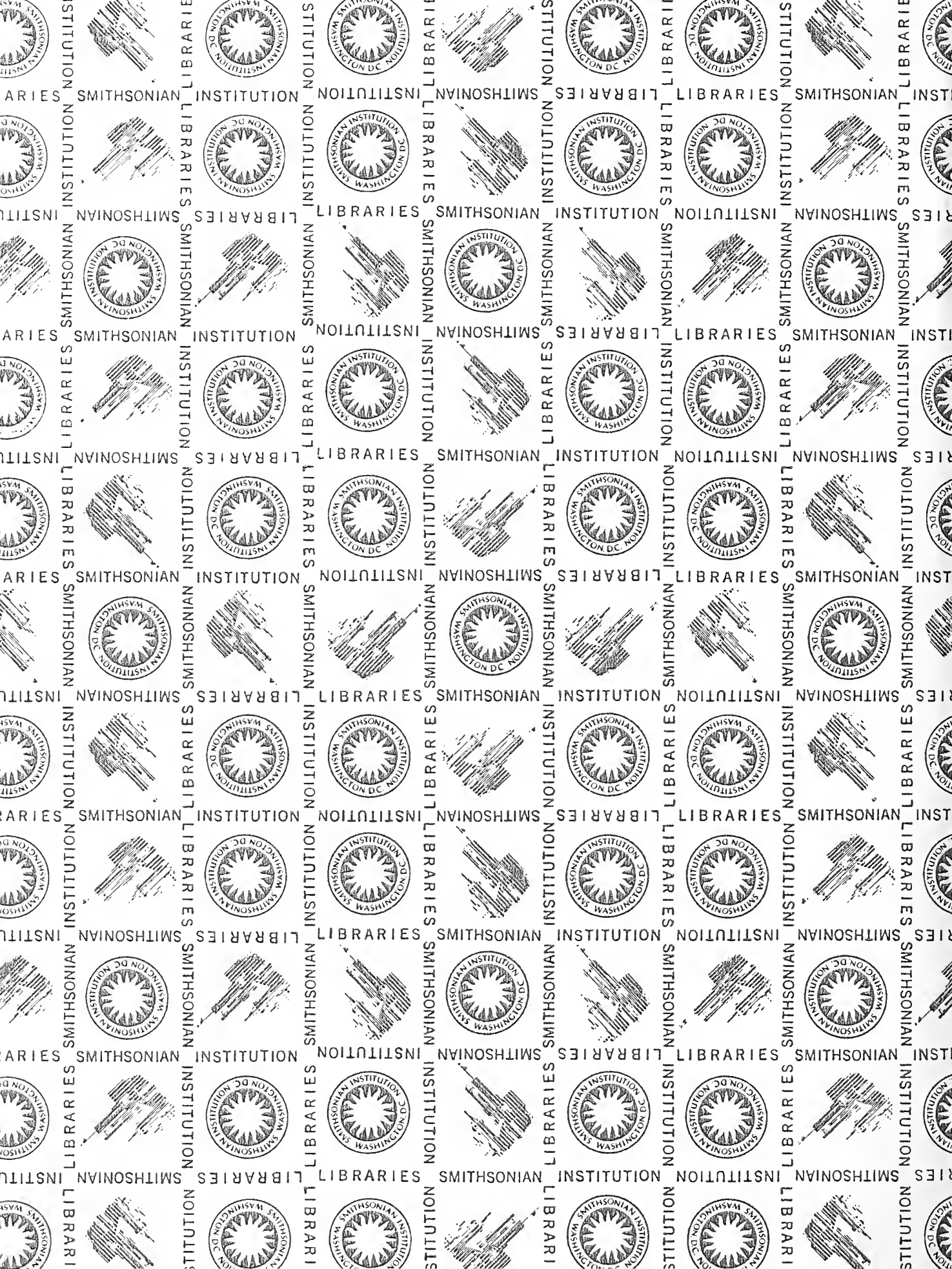
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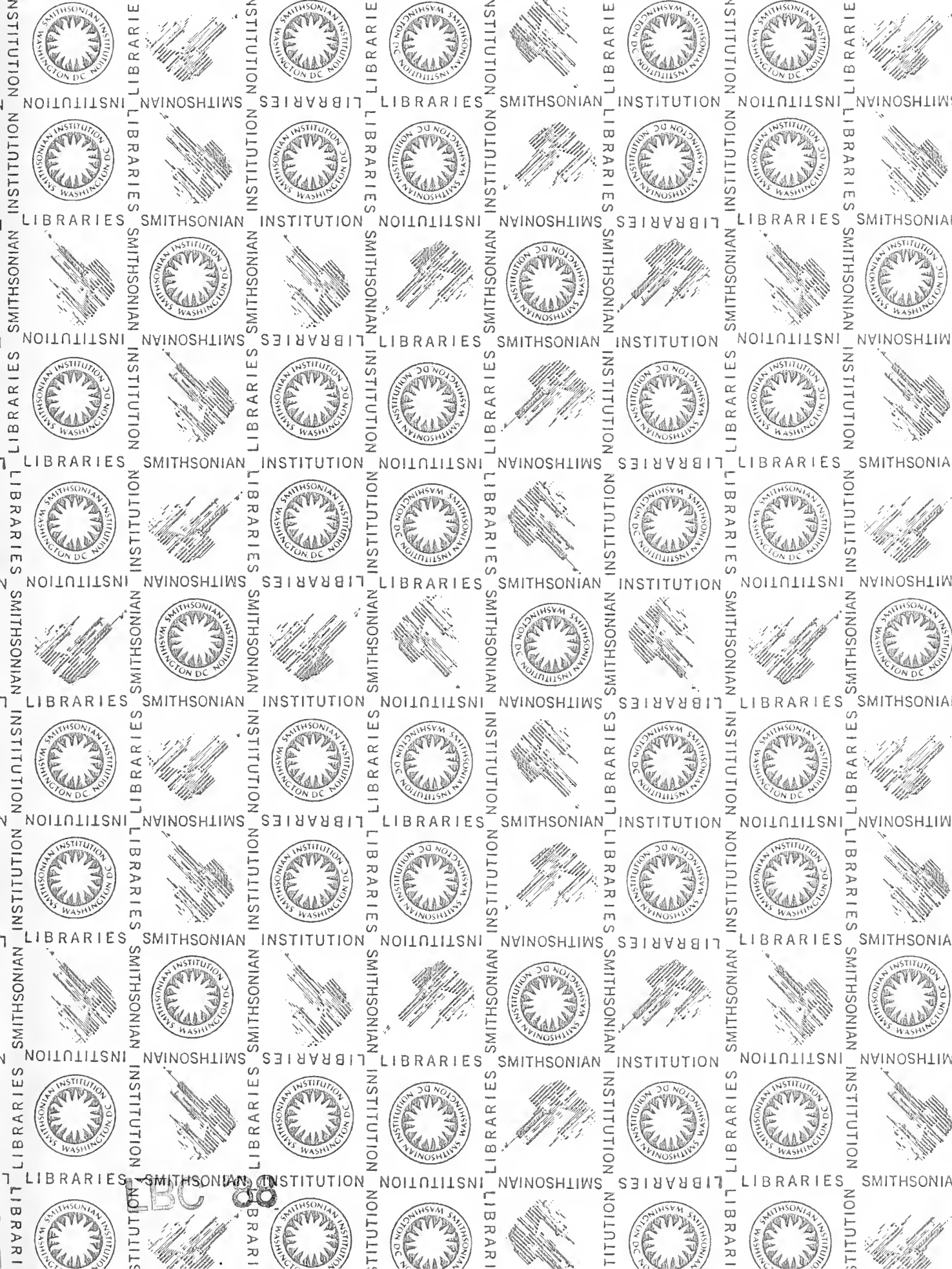
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